UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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Tese de Doutorado

Variação espacial e temporal de espécies arbóreas em florestas da Mata Atlântica: perspectivas sobre o efeito de mudanças climáticas e planejamento de conservação

Rodrigo Scarton Bergamin

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Sul como um dos pré-requisitos para obtenção do título de Doutor em Ciências – ênfase em Ecologia

Orientador: Profa. Dra. Sandra Cristina Müller
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Porto Alegre, junho de 2017.

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Banca Examinadora:
Profa. Dra. Marinez Ferreira de Siqueira
Prof. Dr. João André Jarenkow
Prof. Dr. Gerhard Overbeck

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RESUMO

Distintos padrões de composição de espécies de plantas podem ser observados ao longo de metacomunidades, pois espécies variam de acordo com os diferentes tipos de ambiente e também com a distância geográfica, dado o processo de dispersão. Ainda, estes mecanismos podem causar variação temporal na composição ou abundância de espécies em um sítio devido a alterações que estes mecanismos podem sofrer. Compreender como as mudanças na composição de espécies no espaço, definida como beta diversidade, ou no tempo estão relacionadas ao clima passado, atual ou futuro podem ajudar no planejamento de conservação de uma região. Assim, esta tese esta dividida em quatro capítulos e aborda questões relacionadas com mudanças espaço-temporais na composição de espécies sob uma perspectiva de planejamento de conservação e mudanças climáticas na Mata Atlântica. O primeiro capítulo apresenta um banco de dados com a informação de ocorrência de 1917 espécies de plantas arbóreas distribuídas em 206 comunidades na Mata Atlântica, em diferentes formações florestais (Floresta Atlântica *stricto sensu* (*s.s.*), Floresta com Araucária e Floresta Estacional). O segundo capítulo relacionou padrões de beta diversidade com a efetividade da rede de áreas protegidas nas formações florestais do sul da Mata Atlântica (Floresta Atlântica, Floresta com Araucária e Floresta Estacional). Encontramos altos valores de *turnover* e baixo aninhamento para todas as formações florestais, por isso recomendamos que esforços adicionais precisam almejar o aumento no número de áreas protegidas, especialmente para a Floresta com Araucária e a Floresta Estacional. A maioria das áreas protegidas no sul da Mata Atlântica estão concentradas na região leste, priorizando a Floresta Atlântica *s.s.*.O terceiro capítulo trouxe novas perspectivas sobre a dinâmica da Floresta com Araucária no tempo através da modelagem de nicho ecológica. Durante as flutuações climáticas do Quaternário, estudos palinológicos indicavam uma expansão da Floresta com Araucária, porém nossos resultados demonstraram uma retração da área de cobertura desta floresta, principalmente nas zonas de contato com outras formações florestais. Também observamos que futuramente, se a temperatura continuar aumentando como previsto, a Floresta com Araucária sofrerá uma drástica redução na sua distribuição. Por fim, o capítulo quatro investigou como as espécies de árvores estão respondendo aos efeitos de mudanças climáticas em parcelas permanentes localizadas em ecótonos de florestas Atlânticas. Os resultados mostram que espécies tropicais estão migrando em direção a áreas de maior altitude, ou seja mais frias. Espécies tropicais que já ocorrem em áreas

de Floresta com Araucária estão apresentando maiores taxas de recrutamento e crescimento, e menor mortalidade do que espécies temperadas, características da Floresta com Araucária.

Palavras chave: Floresta Atlântica *strictu sensu*; Floresta com Araucária; Floresta Estacional; beta-diversidade; modelos de nicho ecológico; flutuações climáticas; aquecimento global.

ABSTRACT

Distinct patterns of plant species composition can be observed along metacommunities, as species vary in relation to different types of environment and also to the geographic distance, given the dispersal process. These mechanisms may yet lead temporal variation in species composition or abundance in a given place due to fluctuations on these mechanisms. Understanding how changes in species composition across the space, defined as beta diversity, or in time are related with past, current and future climate changes can help conservation planning in a given region. Thus, this thesis is divided into four chapters and discusses shifts in species composition across space and time under the perspective of conservation planning and climate changes in the Atlantic Forest. The first chapter shows a database with 1917 tree species occurrence distributed in 206 sites across distinct forest formations in the Atlantic Forest biome (Atlantic Rainforest, Araucaria Forest and Seasonal Forest). The second chapter related beta diversity patterns with the effectiveness of the current network of protected areas in southern Brazilian Atlantic forests (Atlantic Rainforest, Araucaria Forest and Seasonal Forest). We found high values of turnover and low nestedness for all forest formations, thus additional conservation efforts must target an increase in the number of protected areas, especially for the Araucaria Forest and the Seasonal Forest. Most protected areas are currently limited to the eastern region and prioritize the Atlantic Rainforest. The third chapter brought new insights about the Araucaria Forest dynamics in time through ecological niche models. During the climatic fluctuations of the Quaternary, palynological studies indicated an expansion of the Araucaria Forest, however our results demonstrated an overall retraction of the cover area, mainly in boundary zones with other forest formations. Yet, we showed that in the future, if the temperature continues to increase as expected, the Araucaria Forest would suffer a drastic reduction in its distribution. Finally, the fourth chapter investigated how tree species are responding to climatic changes in permanent plots located in Atlantic forests ecotones. Our results showed that tropical species are migrating towards to colder areas in higher altitudes. Tropical species that already occur in Araucaria Forest areas are even presenting higher rates of recruitment and growth, and lower mortality than temperate species characteristics from the Araucaria Forest.

Key words: Atlantic Forest *strictu sensu*; Araucaria Forest; Seasonal Forest; beta-diversity; ecological niche models; climatic fluctuations; global warming.

SUMÁRIO

INTRODUÇÃO GERAL

Fatores que determinam mudanças espaço-temporais na composição de espécies de plantas sempre foi um tema que despertou grande interesse dos pesquisadores. Entender os padrões que geram variações espaciais e temporais na vegetação é fundamental para a compreensão da dinâmica vegetacional (Delcourt et al. 1983). A teoria de nicho afirma que as espécies não estão distribuídas espacialmente ao acaso, portanto, variações nas condições ambientais entre diferentes sítios resultam em comunidades estruturadas devido aos diferentes requerimentos de nicho entre as espécies (Wright 2002). Por outro lado, o processo de dispersão estrutura as comunidades no espaço devido a limitação das espécies em se dispersar e colonizar novos ambientes (Hubbel 2001). Ambos os processos podem também acarretar mudanças na composição de espécies no tempo, pois as condições ambientais em um dado local podem mudar (e.g. aumento da temperatura), possibilitando assim a ocorrência de espécies que antes não estavam presentes dadas as condições climáticas. Variações temporais nas taxas demográficos das populações e no processo de dispersão também influenciam o processo de colonização das espécies (Chave 2008).

A mudança na composição de espécies no espaço e no tempo é definida como beta diversidade (Anderson et al. 2006; Ruhí et al. 2017). O conhecimento sobre os padrões de beta diversidade podem ajudar a decidir o número, a localização e o tamanho das áreas protegidas necessárias em uma dada região a fim de maximizar a proteção da biodiversidade. Regiões onde a beta diversidade é alta, como por exemplo a Mata Atlântica, um grande número de áreas protegidas seria necessário para conservar a biodiversidade regional. Além de um grande número de áreas protegidas, o arranjo espacial destas é crucial para a conservação das espécies pois altas taxas de beta diversidade podem implicar em uma rede de áreas protegidas próximas para maximizar a conservação da biodiversidade. Outro argumento importante para uma rede de áreas protegidas próximas são as mudanças climáticas induzidas pelo homem, especialmente em regiões ecotonais. As mudanças climáticas estão causando mudanças na distribuição das espécies em direção a áreas mais frias, como os polos e regiões de altitudes elevadas (Parmesan e Yohe 2003). Neste sentindo, áreas protegidas próximas podem facilitar a expansão das espécies, protegendo locais potencias para onde a espécies podem migrar para novos ambientes (Lemes e Loyola 2013).

Com relação às mudanças climáticas, compreender como estas vão impactar os ecossistemas naturais tem sido considerado um dos maiores desafios para a comunidade científica, no sentido de criar estratégias eficientes para minimizar e mitigar seus efeitos. Sabe-se que as flutuações climáticas do passado tiveram um papel importante na distribuição geográfica das espécies e dos tipos vegetacionais, causando retração e expansão destas. Neste sentindo, estudos sobre as flutuações climáticas do passado podem ter um importante papel para a compreensão e predição das mudanças na distribuição futura das espécies frente às alterações climáticas previstas nos cenários futuros, como o aquecimento global (Petit et al. 2008). Assim, modelos de nicho ecológico podem ser uma importante ferramenta para investigar os possíveis efeitos que as flutuações climáticas tiveram no passado, bem como, prever os possíveis impactos que as mesmas terão no futuro sobre a distribuição de tipos vegetacionais ou espécies. Contudo, há poucos dados empíricos que suportam as predições dos modelos das respostas das espécies e da vegetação em escalas locais e regionais (Zhu et al. 2012). Portanto, dados provenientes de re-amostragem no tempo, especialmente os de parcelas permanentes, podem fornecer diagnósticos robustos de como reagem as espécies em termos de dinâmica temporal da sua performance , proporcionando assim projeções com maior acurácia em como as mudanças climáticas irão afetar a demografia das espécies no futuro (Dolanc et al. 2013). Como as espécies vão responder de diferentes maneiras frente as mudanças climáticas, identificar quais espécies, em termos de grupos biogeográficos ou funcionais, estarão mais ameaçadas é indispensável para ações de conservação.

Dentro do contexto exposto acima, esta tese visa elucidar algumas questões que envolvem mudanças espaço-temporais na composição de espécies de árvores sob uma perspectiva de planejamento de conservação associada a mudanças climáticas. Para tanto, a tese está divida em quatro capítulos:

Capítulo 1 – Compilation of woody species occurring in the Brazilian Atlantic Forest complex

Muitos trabalhos utilizam base de dados para extrair coordenadas geográficas de ocorrências da espécies, bem como, utilizar as informações de composição de espécies por sítio para buscar padrões gerais de comunidades em escala regional. Contudo, as informações dependem de banco de dados disponíveis, podendo assim comprometer o uso destas informações em áreas pobres em dados, como no caso da Mata Atlântica

(Moilanen 2012). Neste sentindo, o primeiro capítulo apresenta um banco de dados com a informação de ocorrência de 1917 espécies em 206 sítios distribuídos na Mata Atlântica em diferentes formações florestais. Este banco de dados foi utilizado nos capítulos dois e três e está publicado na revista *Frontiers of Biogeography* (Bergamin et al. 2015).

Capítulo 2 – Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Rain Forest

O segundo capítulo buscou relacionar padrões de beta diversidade com o planejamento de conservação. Para tanto, avaliamos a efetividade da rede de UC's para proteger os diferentes tipos florestais no sul da Mata Atlântica (Floresta Atlântica *strictu sensu*, Floresta com Araucária e Floresta Estacional) e propor a expansão desta rede com base nos padrões de beta diversidade e nos níveis de desmatamento e proteção dos três tipos florestais. A beta diversidade de espécies arbóreas foi particionada em substituição (*turnover*) e aninhamento (*nestedness*) para cada tipo de formação florestal. Além disso, examinamos o decaimento da similaridade em razão das distâncias geográficas entre comunidades. Este capítulo está publicado na revista *Biodiversity and Conservation* (Bergamin et al. 2017).

Capítulo 3 - New insights about the dynamics of Araucaria forest through time

O terceiro capítulo buscou elucidar a dinâmica da Floresta com Araucária no tempo. Apesar dos estudos palinológicos indicarem uma expansão da Floresta com Araucária no passado, seus limites de distribuição permanecem incertos devido a limitação espacial destes estudos. Ainda, as previsões de aumento da temperatura ameaçam principalmente os tipos de vegetação que ocorrem em áreas mais frias (Engler et al. 2011), como o caso da Floresta com Araucária. Assim, modelamos a distribuição espacial desta floresta em diferentes janelas de tempo: 1) clima passado, durante o Último Glacial Máximo (cerca de 21,000 anos antes do presente) e Holoceno (cerca de 6,000 anos antes do presente), 2) clima atual e 3) projeções futuras (dois cenários para 2070).

Capítulo 4 - Contrasting responses of tree species in face of climate change in Atlantic Forest ecotones: migrations trends and short-term dynamics

Por fim, o capítulo 4 investigou como espécies e comunidades de árvores estão respondendo aos efeitos das mudanças climáticas em parcelas permanentes localizadas em ecótonos de Florestas Atlânticas. Primeiramente, apresentamos tendências de migração de espécies de árvores em um gradiente altitudinal de Floresta Atlântica. Buscamos elucidar quais espécies estariam mudando sua distribuição para cima das encostas em resposta ao aquecimento global. Segundo, avaliamos mudanças de curto prazo na performance de espécies arbóreas (crescimento, abundância) em comunidades localizadas em áreas de ecótono de Floresta com Araucária e Floresta Atlântica montana através da re-amostragem de parcelas permanentes que foram amostradas há seis anos atrás.

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CAPÍTULO 1

Compilation of Woody Species Occurring in Brazilian Atlantic Forest Complex[#]

Rodrigo Scarton Bergamin[1*], Leandro Da Silva Duarte[1], Vinicius Marcilio-Silva[2], Guilherme Dubal Dos Santos Seger[1], Dieter Liebsch[3] and Márcia C. M. Marques[2]

1-Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 91540-000.

2-Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Brazil, 81531-980.

3- Departamento de Ciências Florestais, Universidade Federal do Paraná, Curitiba, Brazil, 81531-980.

*rodrigo.bergamin80@gmail.com

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Abstract

The Atlantic Forest is a hotspot for biodiversity conservation due to its high level of endemism and threatened areas. Three main forest types, differenced by their floras, compose the Atlantic Forest: Atlantic forest *strictu sensu*, Araucaria Mixed and Seasonal Forests. Their flora is composed by taxa from the Amazon Forest, Cerrado gallery forests, and the Andean region, which makes the Atlantic Forest a relevant study system for ecologists and biogeographers. Here, we present data from 206 floristic checklists describing the occurrence of 1,916 species across the Southern portion of the Atlantic Forest. This dataset can be useful to understand mechanisms underlying plant community assembly process and the historical relationships between different forest formations.

Key words: tropical forest, Araucaria Mixed Forest, Seasonal Forest, Atlantic Forest, community, shrub/tree Species.

Introduction

The Atlantic Forest is the second largest tropical forest in South America. It occurs along the Brazilian east coast and inwards until the eastern Paraguay and northeastern Argentina, covering an area with high climatic variability (Oliveira-Filho and Fontes, 2000) with a remarkable range of latitudinal and altitudinal gradients. Such heterogeneous environments capture a climatic gradient related to annual rainfall (approximately from 800 to 4,000 mm) and mean annual temperatures (averages from 15° to 25°C), which influence species distributions (Scudeller *et al*. 2001, Oliveira Filho *et al*. 2005, Marques *et al*. 2011). According to Oliveira-Filho and Fontes (2000), Atlantic Forest can be classified in two main forms, *sensu strictu* (s.s.) and *sensu lato* (s.l.). The Atlantic Forest s.s. comprises the forests almost distributed in Brazilian coast where local rainfall is influenced by ocean winds and mountain slopes. The Atlantic Forest s.l. includes Seasonal Forests, Araucaria Mixed Forests, Coastal Pioneer Forests (also know as Restinga Forest) and Highland Grasslands.

The Brazilian Atlantic Forest is considered a hotspot for biodiversity conservation (Myers et al. 2000) and shelters about 14000 vascular plants, been 48% of species are endemic (Werneck et al. 2011). Two centers of endemism are main recognized in Atlantic Forest: the northern and the southern (Fiaschi and Pirani 2009). The northern ranges from Rio Grande do Norte to north of Espírito Santo states. This center of endemism shows floristic affinities with Amazon forest and Caatinga. The southern part ranges from Espírito Santo to Rio Grande do Sul states. This part are strongly influenced by elements from others biogeographic origins such as Andean and Austral-Antarctic lineages.

As the southern part of the Atlantic Forest represents an important center of endemism, with floristic differences to the northern part supported by phylogenetic data (Fiaschi and Pirani 2009), here we present a compilation of woody species from this region. Furthermore, we think that the idea of this database is to compare the three main forest types that occur in Southern portion of Atlantic Forest and so, Araucaria Forest does not occur in the Northern portion. In the southern and southeastern Brazilian Atlantic Forest, three main forests types are recognized in the Atlantic Forest Biome: Atlantic Forest *strictu sensu*, Araucaria Mixed Forest and Seasoal Forest.

Atlantic Forest s.s. are associated with the Atlantic coast and include a large area of lowland forests (up to ~ 50 m a.s.l.) and slope forests (~ 50 to 2,200 m a.s.l.) (Figure

1). The climate is heterogeneous, been hot and wet in the lowlands and cold and wetter in the slopes (IBGE 1992, Oliveira-Filho and Fontes 2000). The vegetation in lowlands comprises forests, determined by rainfall and soil sandiness (Marques *et al*. 2011). Among species that determine the vegetation in the coastal plain are *Maytenus obtusifolia*, *Byrsonima sericea*, *Ilex theazans, Calophyllum brasiliense*, *Ocotea pulchella* and *Myrcia multiflora* (Marques *et al*. 2011). In the slopes, forests are highly differentiated by altitude, and species such as *Drimys brasiliensis, Ilex microdonta, Weinmannia paulliniifolia* characterize the vegetation (Bertoncello *et al*. 2011).

Araucaria forests occur in the highland plateau, ranging from 500 m to 1600 m a.s.l. in southern and southeastern Brazil (Klein 1960). The climate is tropical and sub-tropical humid without pronounced dry periods. The annual rainfall ranges from 1400 to 2200 mm, and the annual mean temperature ranges mainly from 12°C to 18°C (Behling 2002). The presence of species phytogeographically related to temperate Austral-Antarctic and Andean floras distinguishes communities within the Araucaria Mixed Forest from more tropical faces of Brazilian Atlantic forests (Rambo 1951). Besides *Araucaria angustifolia*, some other typical species found in those forests are *Podocarpus lamberti* (conifer), *Dicksonia sellowiana* (tree fern), *Drimys* spp. (Winteraceae), and several species of Myrtaceae, and Lauraceae.

Seasonal Forests occurs in the hinterland Parana River basin in the south and southeast Brazil. It is characterized by two distinct seasons with marked alternation from tropical with intense summer rainfalls to subtropical with low winter temperatures and scarce precipitation. During the cold and dry period, 20% to 50% of the canopy trees fall their leaves (deciduous) (IBGE 1992). The mean temperature in the winter is lower than 15º C. The flora of Seasonal forests is often influenced by taxa typical from open areas (Brazilian savannah). This forest type has a dominance of species of *Parapiptadenia, Peltophrum, Cariniana, Lecythis, Tabebuia, Astronium* among others (IBGE 1992).

Compilation of shrub/tree species of Atlantic Forest complex

We present here the compiled information from 206 floristic checklists describing the occurrence of 1,917 shrub/tree species across the geographic range of the Southern Brazilian Atlantic Forest (Figure 1). Floristic data were obtained from published studies (see Appendix 1 for the complete list of published papers) and unpublished information (e.g. PhD thesis and master dissertation). These different sources of data employed distinct survey methodologies, such as floristic surveys, plots and point-centered

quarters, varying in sample efforts, and size criteria for individual inclusion (minimum diameter at breast height, minimum plant height).

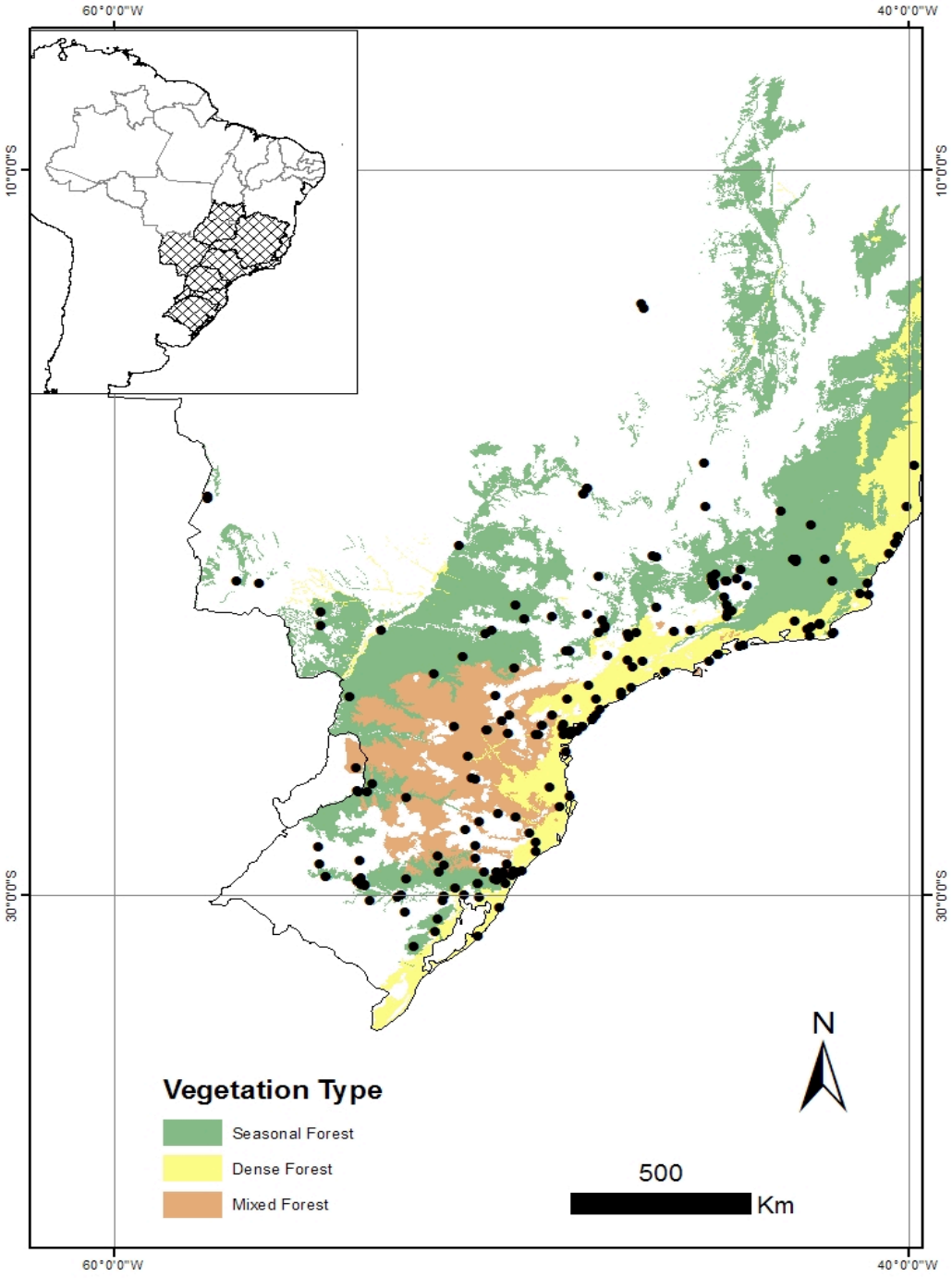

Fig. 1: Distribution of 206 floristic checklists (black points) along the vegetation types of the Atlantic Forest biome (63 Atlantic Forest s.s., 50 Araucaria Mixed Forest, and 96 Seasonal Forest). Points outside of the highlighted vegetation types, are forests areas (Seasonal Forest or Araucaria Mixed Forest) occurring over open ecosystems such as grasslands, Pantanal and Cerrado (savannah).

Structure of the database

We compiled information from 206 floristic checklists, presented in dataset (Site_info.txt), describing the occurrence of shrub/tree species (Species_sites.txt) across the geographic range of the Southern Brazilian Atlantic Forest biome (63 Dense forests, 50 Mixed forests, and 96 Seasonal forests).

Sites information

-Identity: Sites_info.txt

-Size: 207 rows (sites, including header) and 10columns (site descriptors, including header)

-Format and storage mode:Tab-delimited ASCII text (.txt).

-Header information: Table 1 describes the information given in the header.

Table 1. Summary of variable information for file sites_info.txt.

Variable	**Variable definition**	**Units of measurement**	**Data type**	**Codes for character data**
Cod.	Unique identifier for each site	NA	Character	NA
Vegetation type	Atlantic forest type that characterizes the site	NA	Character	Dense Forest: Dense Rain Forest; Mixed Forest: Mixed Rain Forest; Seasonal Forest: Seasonal Deciduous and SemideciduousForest .
Site	Site location (City or Protect area name)	NA	Character	NA

State	Define the Brazilian State where site is placed	NA	Character	NA
Lat	Latitude data of study sites were extracted from original studies	°	Numeric	NA
Long	Longitude data of study sites were extracted from original studies	°	Numeric	NA
Inclusion	The inclusion criteria for plants in this site	NA	Float	All shrub/tree spp: All shrub and trees species are sampled. DBH ≥ "x": Only shrub and tree species with diameter at breast height equal or taller than a specified value "x".
Method	Method of	NA	Character	Plot: plot sampling method

	sampling			Floristic: Floristic inventory sampling method. Point: Point centered quarter sampling method
Effort	Describe the total sampling area (m²) or number of points for site	NA	Float	NA
Source	Simple citation of the data source (Complete references in metadata)	NA	String	NA

Plant community composition

-Identity: Species_sites.txt

-Size: 1,917 rows (species, including header) and 207 columns (sites, including header).

- Format and storage mode:Tab-delimited ASCII text (.txt).

- Header information: The first variable in the header ("Species") indicates species name. Headers in columns 2–207 name the sites.

The first variable in the header ("Species") indicates species name. Variables in columns 2–207 describe the occurrence (1: present, 0:absent) of each plant species in each site. We follow for botany nomenclature presented in the Missouri Botanical

Garden (http://www.tropicos.org) and Flora do Brasil databases (http://floradobrasil.jbrj.gov.br) in 2013. We crossed the information of these two websites because for many plant families, Flora do Brasil does not provide the synonyms of the species.

Potential uses for Compilation of Woody Species Occurring in Brazilian Atlantic Forest Complex

This dataset is useful to understand mechanisms underlying plant community assembly process and the historical relationships between different closed distributed forest formations. The analyses of phylobetadiversity among forest types using this dataset (Duarte et al. 2014) showed a differentiation in phylogenetic composition among forest, with a higher phylogenetic diversity in Araucaria Mixed forest. This kind of approach is important, for example, for a wider interpretation of species conservation in Brazilian Atlantic forest. The information of the species occurrence, agreed with GIS layers, can help to produce the range of species distribution. Moreover, the data could be used to calibrate environmental niche models and project them into past or/and future distribution of target species in different climate scenarios.

Publications using the data set:

Duarte, L.D.S., Bergamin, R.S., Marcilio-Silva, V., Seger, G.D.D.S., Marques, M.C.M. (2014) Phylobetadiversity among Forest Types in the Brazilian Atlantic Forest Complex. PLoS ONE, 9(8), e105043. doi:10.1371/journal.pone.0105043

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CAPÍTULO 2

Linking beta diversity patterns to protected areas: Lessons from the Brazilian Atlantic Rainforest[#]

Bergamin, R.S[1,2,4].; Bastazini, V.A. G.[3]; Vélez-Martin, E.[3]; Debastiani, V.[3]; Zanini, K.J.[1]; Loyola, R. [2]; Müller, S.C[1].

1- Plant Ecology Lab, Graduate Program in Ecology, Universidade Federal do Rio Grande do Sul.

2 - Conservation Biogeography Lab, Department of Ecology, Universidade Federal de Goiás.

3 - Quantitative Ecology Lab, Graduate Program in Ecology, Universidade Federal do Rio Grande do Sul.

4- Corresponding Author: rodrigo.bergamin80@gmail.com, +55 51-33086777, Fax: +55 51-33087623.

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Abstract

Understanding the processes that drive patterns of beta diversity is crucial for planning conservation policies and for designing networks of protected area (PAs). Beta diversity can be decomposed into two components: 1- species turnover, the replacement of species by others resulting in a low proportion of shared species; 2- species nestedness - the result of differences in species richness, when a poorer community is a subset of species from a richer community. We aimed to evaluate beta diversity patterns and how they are represented in the network of PAs in southern Brazilian, regarding three forest types: Atlantic Forest *stricto sensu* (*s.s.*), Araucaria Forest, and Seasonal Forest. Beta diversity was partitioned into the turnover and nestedness components. Additionally, we examined spatial patterns of site similarity using distance decay curves. Beta diversity was mainly caused by species turnover (approx. 86%), with only a small contribution of nestedness (approx. 5%) in all three forests types. The patterns of distance decay curves revealed that even at small distances (50–100 km), we found a considerable decrease in similarities, reinforcing turnover patterns. As turnover brought the larger contribution to beta diversity, additional conservation efforts must target an increase in the number of PAs, that should be spread across each one of the regions, to maximize the protection of species diversity. Most of the PAs are currently limited to the eastern region and prioritize the Atlantic Forest *s.s.* Thus Araucaria Forest and Seasonal Forest should deserve special priority in new conservation actions, as they also contain high levels of species turnover.

Key words**:** Biodiversity conservation; Nestedness; Turnover; Spatial conservation planning.

Introduction

Spatial analyses of quantitative data improve conservation planning and the design of networks of protected area (PAs). Different spatial prioritization techniques have been developed (Margules and Sarkar 2007; Moilanen et al. 2009) taking into account principles like representativeness, complementarity, persistence, vulnerability and flexibility (Wilson et al. 2009). Their use has granted higher cost-efficiency and decreased the gap between science and decision-making. However most of these methods, including target-based systematic conservation planning (Sarkar and Illoldi-Rangel 2010) and spatial priority ranking (Moilanen et al. 2011), rely on available species distribution data, compromising their use in data-poor areas like in the Brazilian Atlantic Rainforest (Moilanen 2012).

Beta diversity defined as the variation in species composition between sites (Anderson et al. 2006) should be an important tool for conservation planning. However, contrary to alpha diversity that has attracted much attention from theoretical and applied ecologists and practitioners (O'Brien et al. 2011), little attention has been given to beta diversity in the selection of protected areas (PAs) (Fairbanks et al. 2001). Knowledge on beta diversity patterns can aid to decide the number of PAs needed and their size (Wiersma and Urban 2005), going beyond the systematic conservation planning approach that only considers the location of PAs in relation to natural physical and biological patterns (Margules and Pressey 2000). The efficiency of PA networks depends not only on species richness, but also on how well the complementarity among sites increases the conservation of gamma diversity (Howard et al. 1998; Bush et al. 2016; Socolar et al. 2016).

Beta diversity can be decomposed into species turnover and nestedness (Baselga 2010). Species turnover is the replacement of some species by others resulting in a low

proportion of shared species between two communities where turnover is high. On the other hand, species nestedness represents the differences between two communities only in terms of species richness, with the poorer community as a subset of the richer one. While a nested pattern indicates that only some species are able to occur over all site conditions, turnover patterns are associated to environmental heterogeneity and variability in species attributes, where new occurrences are associated to distinct local conditions coupled with distinct dispersal abilities (Ulrich and Almeida-Neto 2012). If species turnover is the main pattern of beta diversity, a larger number of PAs would be necessary to conserve regional biodiversity. Otherwise if nestedness is the main pattern, one large protected area comprising a high species richness could be sufficient.

Brazil's Atlantic Forest is a biodiversity hotspot (Mittermeier et al. 2011) and is among the most threatened tropical forests in the world (Oliveira-Filho and Fontes 2000). Originally it covered about 150 million ha, but nowadays only 11.7% of the vegetation remains in an extremely fragmented landscape, where most fragments are smaller than 50 ha (Ribeiro et al. 2009). Nevertheless, the Atlantic Forests continue to be deforested at impressive rates of 20,000 ha per year (SOS Mata Atlântica 2014). Establishing a system of PAs play an important role in conservation biodiversity and ecosystem function (Gaston et al. 2008), especially when the drivers of habitat loss remain uncontrolled. The PAs of strict protection (classified as "*proteção integral"* in Brazil and equivalent to IUCN categories I-IV) in the Atlantic Forests protects a small portion of the remaining forests. It covers approximately 2.26 million ha (Ribeiro et al. 2009), which represents only 1.62% of the original area. Adding up the sustainable use PAs (IUCN categories V-VI), the total conserved areas rises to 10.7% (Fonseca et al. 2010). Although the Atlantic Forests are within the regions with the largest number of PAs in South America (Tabarelli et al. 2005), a comprehensive knowledge on the

efficiency of the current PAs system remains unevaluated. Some studies has warned that it will not be effective in face of climate changes (Loyola et al. 2012, 2014; Ferro et al. 2014; Lemes et al. 2014) and many of these PAs are spatially biased and clustered, compromising the representativeness. For example, in southern Brazilian Atlantic Forests (Fig.1) the three different forest physiognomies (Atlantic Forest *s.s.*, Araucaria Forest, and Seasonal Forest) show unbalanced levels of protection.

In this paper, our main aim is to evaluate the effectiveness of the network of PAs in southern Brazilian Atlantic Rainforests to protect the three main forest types: Atlantic Forest *s.s.*, Araucaria Forest, and Seasonal Forest and propose its expansion based on beta diversity patterns and levels of deforestation and protection. Beta diversity patterns of tree species were evaluated for each forest type regarding the relative importance of species turnover and nestedness and also through the floristic similarity decay against the geographic distances between communities. As we can find high floristic variation both among and within the different Atlantic Forest types (Oliveira-Filho and Fontes 2000; Marques et al. 2011; Bergamin et al. 2012; Stival-Santos et al. 2015), we expect species turnover to be the main component of beta diversity patterns. Accordingly, several and spatially well-distributed PAs would be necessary to conserve plant diversity. Finally, we evaluated the current spatial distribution of PAs of the studied region to discuss it under the light of the beta diversity and deforestation patterns of the considered forest types.

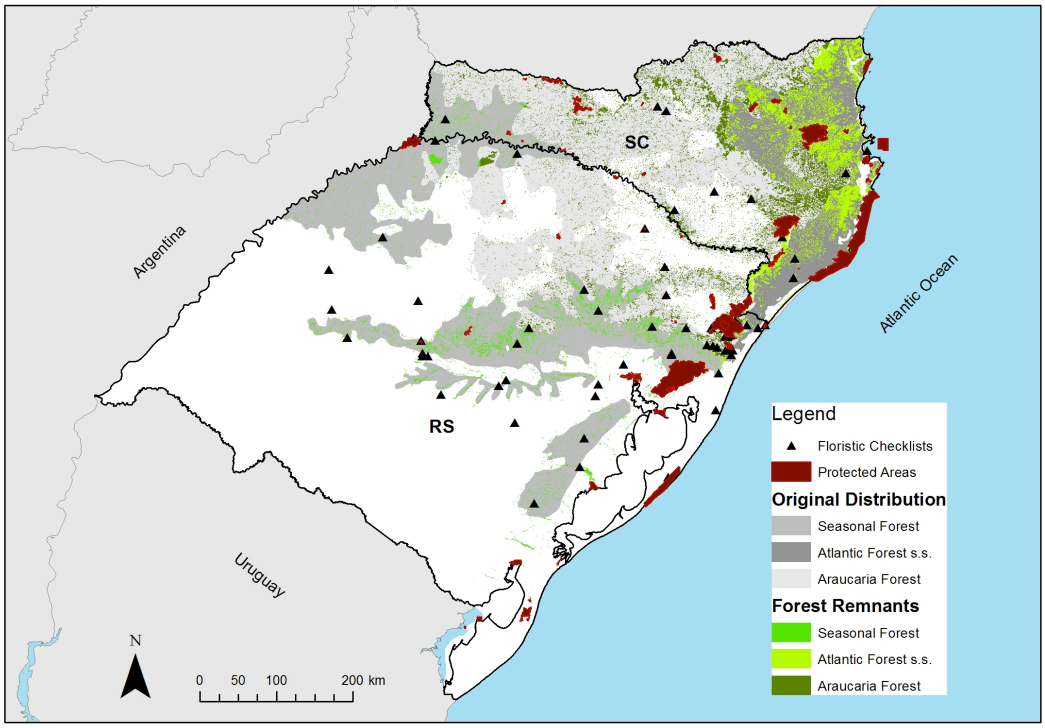

Figure 1. Distribution of the floristic surveys, strictly and sustainable protected areas, original distribution and forest remnants of the three forest types in southern Atlantic Forests. Triangles outside of the highlighted vegetation types are forests patches (Seasonal Forest or Araucaria Forest) occurring in a grassland matrix.

Methods

Study region

The Atlantic Forests extend along the Brazilian eastern coast and inwards to eastern Paraguay and northeastern Argentina across several climatic zones (Oliveira-Filho and Fontes 2000). It consists of different forest types with environmental gradients strongly influencing their floristic variation, causing a continuum of species replacement among forest types (Marques et al. 2011; Bergamin et al. 2012). In southern Atlantic Forests, defined here as the forest in the two southernmost states of Brazil (Rio Grande do Sul and Santa Catarina), the climate is subtropical and there are three main forest types: the Atlantic Forest *s.s.,* comprising only the coastal rain forest in areas of lowland and

mountain slopes (0 m to 2200 m a.s.l.), with a high diversity of plant species; the Araucaria Forest, distributed predominantly on the southern Brazilian Plateau and characterized by the conspicuous *Araucaria angustifolia* (Bertol.) Kuntze species; the Seasonal Forest is characterized by the deciduousness of many canopy trees (20% to 50% shed their leaves during winter).

Species composition, forest remnants, and protected areas data

We obtained data from a compilation of 77 floristic surveys (Table S1) containing the occurrence of tree species in southern Atlantic Rainforests (21 in Atlantic Forest *s.s.*, 24 in Araucaria Forest and 32 in Seasonal Forest). As the floristic studies used distinct methods (supplementary material), we only considered species presence data. Unidentified and exotic species were not included in the floristic list. Forest sites represent well-conserved forest remnants and exotic species were exceptions. Recent synonyms were checked in the Missouri Botanical Garden website (http://www.tropicos.org). The final compilation resulted in a database with 77 sites containing 511 species.

The levels of deforestation and protection for the three forest types were quantified considering the forest remnants map (SOS Mata Altântica 2008). To calculate deforestation we overlaid it with former distribution data from Brazil Vegetation Map (IBGE 2004), and to calculate protection we overlaid it with current official limits of PAs in the enforcement area of the Atlantic Forest Biome (MMA 2011). Disparities in the extent of forest loss and protection among the forest types were identified through the Conservation Risk Index (CRI), which is the ratio of percent area converted to percent area protected. This index produces a relative risk value of biodiversity loss (Hoeckstra et al. 2005). We then calculated the mean Euclidean distance among the geographic centroid of PAs to understand the level of clustering of

PAs within each forest type and further compare them. To avoid distortion in distance and area measures, all spatial data were previously converted to Albers Equal-Area Conic projection.

Data analyses

We used Sørensen-based multiple-site dissimilarity (Baselga 2010) to estimate the total beta diversity for each forest type and in all cases total beta diversity was partitioned in turnover and nestedness additive components. Araucaria Forest and Seasonal Forest had more sites than Atlantic Forest *s.s.*, for this reason we standardized the number of sites of each forest type to 21 (randomly chosen) to deal with a similar sampling effort. We then computed the multiple-site components of nestedness, turnover, and total beta diversity. We repeated this procedure 1000 times to obtain the mean and the standard deviation of each component of beta diversity. These analyses were carried out in the R package 'betapart' (Baselga et al. 2013).

To calculate the floristic dissimilarity decay along geographic distances (the spatial gradient) for each forest type we used the Sørensen dissimilarity index (Sørensen 1948; Koleff et al. 2003). It measures the proportion of species shared between two communities, ranging from 0 to 1, where 1 is the maximum dissimilarity with no shared species between two communities. It also can be partitioned into additive components, representing the pure spatial turnover and the nestedness component (Baselga 2010). We then evaluated four possibilities to fit the best model of community dissimilarity decay for each forest type: linear, asymptotic, exponential and a null model containing only the intercept (Nekola and White 1999), and compared them through an information-theoretic framework (Burnham and Anderson 2002; Anderson 2008). The shape and slope of distance decay curves may provide hints of how strongly is the species similarity spatially limited through a region, which can be associated to

differences in environmental conditions (species sorting), in the dispersal rate of organisms (distinct traits), or even to the neutral theory (ecological drift and random dispersal that decrease with the distance) (Soininen et al. 2007). We measured the plausibility of each candidate model using second order Akaike Information Criterion (AICc) (Johnson and Omland 2004; Anderson 2008). The AICc is an estimate of the expected Kullback–Leibler information lost by using a model to approximate the process that generated the observed data, corrected for small samples (Johnson and Omland 2004). Next, we calculated the delta AICc (ΔAICc), which is the distance between each model and the best one, and the Akaike weight for each model (w_i), which is the probability that model *i* is the actual Kullback-Leibler best model in the set (Burnham and Anderson 2004; Johnson and Omland 2004). Model selection analyses were carried out using the R package 'bbmle' (Bolker 2010).

Results

We found that beta diversity of tree species of Atlantic Forests in southern Brazil is mainly due to species turnover, with only a very small contribution of nestedness in all forest types (Table 1). The exponential function was the best-fitted model to represent the distance decay for all forest types (Table 2, Fig. 2). Highest similarities were concentrated within a short range of nearly 25 km and after 100 km, the similarity decayed at slower rates. For distances higher than 50 km, mean similarities were lower then 0.4, indicating a high turnover for all forest types. The Atlantic Forest *s.s.* showed the highest turnover with the lowest slope smooth and a similarity value around 0.2. The Seasonal Forest showed the lowest turnover with the highest slope smooth and a similarity value around 0.4. The Araucaria Forest showed intermediary values but a steeper slope when compared with the other forest types.

Table 1: Beta diversity, decomposed into turnover and nestedness components, percentage of deforestation, level of protection within PAs (percentage of original distribution, forest area, number of protected areas and mean distance) and conservation risk for the Altantic Forest types. βsor is the total beta diversity, βnes is the nestedness component, βsim is the turnover component, n is the number of PAs, d is the mean distance among PAs and CRI is the Conservation Risk Index.

Forest type	**βsor**	**βnes**	**βsim**	**Deforestation %**	**Protection (PAs)**				**CRI**
					%	**km^2**	**n**	**d (km)**	
Atlantic Forest *s.s.*	0.912	0.047	0.866	56.4	8.24	2,260	24	194	7
Araucaria Forest	0.904	0.037	0.867	80.1	0.91	678	23	201	88
Seasonal Forest	0.895	0.056	0.839	89	0.44	248	16	286	204

Table 2: Model selection using second order Akaike Information Criterion (AICc). Degrees of freedom (DF), Delta AICc (ΔAICc), and Akaike weight (Weight).

Forest Type/Model				
Atlantic Forest *s.s.*	AICc	DF	ΔAICc	Weight
Exponential	-265.8	3	0	0.67
Linear	-264.3	3	1.4	0.33
Asymptotic	-223.3	3	42.4	<0.001
Null model	-209.4	2	56.3	<0.001
Araucaria Forest				
Exponential	-449.7	3	0	0.99
Linear	-417.9	3	31.8	<0.001
Asymptotic	-392.1	3	57.7	<0.001
Null model	-343.7	2	106.0	<0.001
Seasonal Forest	AICc	DF	ΔAICc	Weight
Exponential	-946.7	3	0	0.99
Linear	-932.0	3	14.7	<0.001
Asymptotic	-894.3	3	52.3	<0.001
Null model	-867.4	2	79.2	<0.001

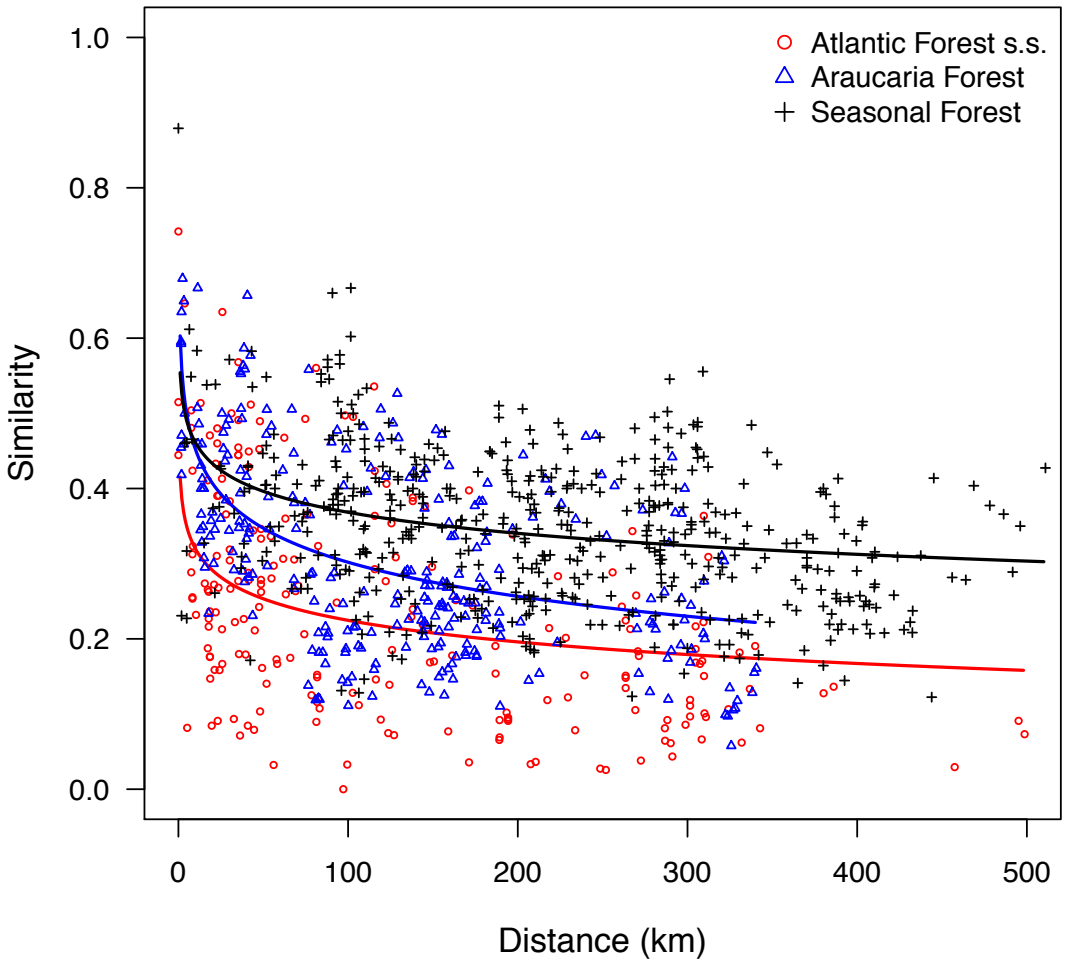

Figure 2. Decay of species similarity (Sørensen index) as a function of geographical distance between pairs of tree species communities (21 for each type) of three forests types (Atlantic Forest *s.s.*, Araucaria Forest, and Seasonal Forest) in the southern Atlantic Rainforests. The exponential curve was the selected adjustment for all forest types, based on AICc (see also Table 2).

The three forest types showed high levels of forest suppression but the Seasonal Forest has been the most vulnerable, as a consequence of both highest levels of deforestation and lowest levels of protection (huge value of CRI). The Atlantic Forest *s.s.* had the lowest conservation risk (CRI= 7) with 11.951 km^2 within protected areas, which represent 8.2 % of the original distribution. The two other forest types remain with low levels of protection (less than 1% within protected areas) (Table 1).

The average distance between PAs was lower in the Atlantic Rainforest *s.str.* (194 km) and higher in the Seasonal Forest (286 km). The Araucaria Forest showed an intermediary average distance of 201 km (Table 1).

Discussion

As many studies have reported a continuum of species replacement between sites in southern Atlantic Forests due to environmental factors (Oliveira-Filho and Fontes, 2000; Marques et al. 2011; Bergamin et al. 2012; Oliveira-Filho et al. 2013; Stival-Santos 2015), the high degree of beta diversity for the three forest types found in our study is not surprising. However, the high rates of species turnover in each forest type in relation to nestedness bring new insights on the current spatial arrangement of PAs in southern Atlantic Forests. As turnover is the main component driving beta diversity patterns, conservation efforts must target a large number of PAs distributed throughout the distribution range of each forest type to maximize tree species conservation and probably many other life forms associated with them (Baselga 2010; Socolar et al. 2016). Furthermore, the degree of complementarity (Howard et al. 1998) of tree species among sites is crucial to conservation, once that biodiversity is represented by a set of conserved sites and not a simple accumulation of individual richness values (alpha diversity) (Bush et al. 2016). Despite the differences in tree species richness among sites of each forest type (55±28.4 for Atlantic Forest *s.s.*; 45.9±17.8 for Araucaria Forest; 47.3±23.6 for the Seasonal Forests), nestedness contributed with a small fraction of the total beta diversity. So by conserving only the most species-rich sites, we are not capturing the spatial variation, which might be highly detrimental for long-term regional conservation. These results and concerns are similar to those pointed out by Fairbanks et al. (2001) who suggested that an increase in the

number of PAs was necessary in the Eastern coast of South Africa to turn the conservation of bird communities more effective.

Our distance decay curves reinforced that even at small distances (< 50 km) we have a considerable decrease in tree species similarities, highlighting the importance of beta diversity for regional patterns of tree species composition. Although different processes may support such decay patterns, a recent broad study in a nearby Atlantic Forest region found that environmental differences contributed much more to species dissimilarities than pure geographical distances, asserting the importance of species sorting processes (Stival-Santos et al. 2015). This lead us to assert that beyond the need of several PAs they should be as close to each other as possible, given the possibilities under the current fragmentation scenario, but spatially spread in the landscape (not clumped in a region) in each forest type to maximize biodiversity conservation.

Distance decay studies are highly sensitive to grain size and study extent, with macroecological studies exhibiting lesser steep declines than small spatial extent studies (Steinbauer et al. 2012), which could partially explain the observed pattern of our study. However, the high degree of tree species rarity in the Atlantic Forest (Scudeller et al. 2001; Caiafa and Martins 2010) plays an important role in regulating species turnover and it can also explain the distance decay patterns here observed. Caifa and Martins (2010) analyzed 846 tree species from the southern portion of the Brazilian Atlantic Forest and suggest that 54% showed some form of rarity. Furthermore, we believe that fine grain studies may bring new insights about how species diversity responds to microhabitats potentially related to biotic factors and how it is structured across space.

In view of the results, the actual picture of the spatial arrangement of PAs in southern Atlantic Forests is worrisome. Even though the Atlantic Forests have probably the largest number of PAs in South America compared to other biomes (Tabarelli et al.

2005), the number of PAs and their spatial arrangement has been pointed out to be insufficient to safeguard species diversity and related processes (Tabarelli et al. 2010; Lemes et al. 2014). Huge gaps of unprotected areas can be observed when we analyze the spatial arrangement of PAs and the average distance between them, which likely represent gaps in species representativeness. Among the three forest types, the Atlantic Forest *s.s.* is somewhat better protected than the others with 8.24% of remaining forest under protection, which gives the lowest CRI among the forest types. However, linking the average distance between PAs and the pattern of its distance decay curve, there still are gaps to fill by adjusted conservation plans. The average distance between PAs of Atlantic Forest *s.s.* is 194 km, but its similarity decay fast in smaller distances, with a slope smooth around 100 km and a proportional change of circa 20% in species composition similarity.

Considering the Araucaria Forest, these gaps seems to be greater, as only 0.91% of the remaining forest are under official protection and the species similarity also decays fast. Its decay curve revels a change of 30% in the similarity after 100 km of distance. In addition, the average distance between PAs was 201 km. The eastern region of Araucaria Forest is better protected than the western, where the PAs are much scarcer (see Fig. 1). As the east-western environmental gradient produces a continuum of species replacement in this forest (Gonçalves and Souza, 2013), many trees and associated species might be at risk. Ultimately, the Seasonal Forest can be considered in a situation even worse. With only 0.44% of the remaining forest under protection, the average distance between PAs is 286 km. Therefore the gaps of PAs in this forest type are much higher, once that around 90 km the proportional change in species composition similarity is 15%. It is noteworthy that both forest types have high CRI. However, Seasonal Forest presents an outstanding value of CRI due to levels of

deforestation and few remaining forest in PAs. Fragmentation strongly influences plant community composition due to habitat loss (Jamoneau et al. 2012; Collins et al. 2016). In conjunction, deforestation and fragmentation influence the size of forest remnants since in small fragments increased edge area affects community composition by promoting the proliferation of widespread, disturbance-tolerant species (Tabarelli et al. 2012; Collins et al. 2016), while large fragments shelter shade-tolerant species. Furthermore, as isolation among fragments increases, species turnover should be more prone to be determined by species dispersal and the size of the species pool of each region (Laurance et al. 2007). Thus, the high levels of species turnover for Araucaria and Seasonal Forest could be linked to the high level of habitat loss and fragmentation.

Beyond increasing the number of PAs, their spatial arrangement is crucial if conservation of forest biodiversity is to be achieved. One of the long-standing patterns recognized in ecology is that species composition similarity decays as a function of geographical distance (Nekola and White 1999). Thus, one might expect that the farther two PAs are, the more species are being protected. However, our results show that a network containing PAs close to each other is necessary to maximize conservation in these forest types, given the outstanding rates of tree species turnover. An additional argument for a closely-knit network of PAs is the current human-induced climate change. In times when climate changes are causing shifts in species distribution, *e.g.* to higher latitudes and elevations (Parmesan and Yohe 2003), PAs close to each other may play a critical role for biodiversity conservation, once they can facilitate species expansion by protecting potential habitats for colonizers of species that are shifting into new ranges (Thomas et al. 2012; Ferro et al. 2014; Lemes et al. 2014).

While we show the need of more PAs to protect southern Atlantic Forests, the current political situation appears to be little favorable for this. Bernard et al. (2014)

showed that from 1981 to 2012 PAs in Brazil suffered from downsizing, downgrading or degazzeting. Considering the 7,289,214 ha of PAs spread across the Brazilian territory, 53.9% suffered a reduction in their area (downsized), 20.8% were downgraded (decrease of legal restrictions on the number, magnitude, or extent of human activities within the PA), 17% were degazetted (PA loses completely its protection status and no longer exists as a PA), 7.8% were reclassified (category of PA change), and 0.5% was upgraded (increase of legal restrictions). Data as that shown by us reveal the risks associated with these practices for conservation even more clearly. However, the Native Vegetation Protection Law (defined in Law number 12,651 on May 25, 2012 and altered by Law number 12,727 from October 17, 2012), which replaced the Forest Code from 1965, brings some potential positive consequences (despite some negative ones too, which are not discussed in this paper; see Brancalion et al. 2016) to biodiversity conservation. One of the advances is the Environmental Rural Registry that is an online registry system for rural properties and rural holdings with their status in relation to the law demands (Brancalion et al. 2016). Following this, landowners must have a minimal of native vegetation covering areas of permanent protection (such as steep slopes, hilltops, water springs, streams, pounds, reservoirs, costal shrublands and mangroves) and 20% (in the case of Atlantic Forests) of legal reserve, which limit the conversion and the use of the vegetation. Such actions could ensure a broader protection of the biodiversity, increasing the connectivity between PAs and attending beta diversity into conservation planning, since 90% of the Atlantic Rainforest biome remnants are located in private areas (Brancalion et al. 2016).

The fact that most of the PAs are limited to the east region and prioritizes Atlantic Forest *s.s.* is probably a result of conservation strategies based on specific taxa, as "flagship taxa" (Rezende et al. 2015), or on local richness (alpha diversity).

However, even more PAs would be necessary to this forest type if we take into account patterns of beta diversity and the regional diversity. However, the Araucaria Forest and the Seasonal Forest are in an even worse situation, as pointed out by the CRI, and urgently need more conservation efforts like increase the number of PAs. They showed similar levels of turnover and distance decay as the Atlantic Forest *s.s.*, but both have lower levels of remaining forest under protection and PAs that are too far from one another. While these forest types are included in the Biodiversity Hotspot Atlantic Forest (Mittermeier et al. 2011), but they been neglected in terms of conservation, despite high levels of deforestation. Finally, when we think about expand the network of PAs in Atlantic Forests, Seasonal Forests should be prioritized due to CRI followed by Araucaria Forest. More studies involving other taxa and regions of Atlantic Forests, coupled with beta diversity, are welcome to help the improvement of conservation planning in the southern Atlantic Forest region.

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CAPÍTULO 3

New insights about the dynamics of Araucaria forest through time[#]

Rodrigo S. Bergamin [a,b], Vanderlei Debastiani [c], Daiany Joner [b], Priscila Lemes [d], Taís Guimarães [e], Rafael Loyola [b,f], Sandra Müller [a]

[a] Laboratório de Ecologia Vegetal, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil;

[b] Laboratório de Biogeografia da Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, Goiás, Brazil;

[c] Laboratório de Ecologia Quantitativa, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil;

[d] Laboratório de Herpetologia, Departamento de Zoologia, Universidade Estadual Paulista "Júlio de Mesquita Filho, Rio Claro;

[e] Laboratório de Ecologia da Paisagem, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil;

[f] Centro Nacional de Conservação da Flora, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil.

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Abstract

Past global climate fluctuations played a crucial role in determining the distribution of plant species and entire ecosystems by shifting their limits. In this sense, future climatic changes are posed as a threat for the biodiversity by reducing the geographical ranges of species and thus, shifting the distribution of vegetation types around the world. The Brazilian Atlantic Forest is especially understudied concerning the effects of climate changes on species and ecosystem distribution. As composed by different forest types and associated ecosystems, we may expect each vegetation type to respond differently to climate change, mainly those that occur in colder conditions such as the Araucaria forest. To elucidate the dynamics of the Araucaria forest through time, we modeled the spatial distribution of this vegetation type under different climatic scenarios: past climate, during the LGM (*ca.* 21,000 before present) and the Holocene (*ca.* 6000 before present); current climate, and future projections. We also verify the congruence in projected maps modeled through indicator species occurrence and through vegetation type, considering the original distribution of the Araucaria forest based on a vegetation map. The modeling results suggested a retraction of the Araucaria forest from LGM to mid-Holocene and also, from mid-Holocene to the present. Concerning the future predictions, Araucaria forest would suffer a great retraction. Both approaches overall agreed with the retraction of Araucaria forest from LGM and the average congruence of the models generated by species and by vegetation map was 49.60%. Our results allow us to have an understanding about the boundaries of the Araucaria forest past distribution, and corroborate our hypothesis that this forest will likely suffer a great retraction as temperature rise. This pattern is similar to what other studies have found for mountain ecosystems. Additionally, there is evidence that the Araucaria forest is suffering a retraction process since from the past and the models for future scenarios indicate a continuously loss in its coverage probably at the expense of the expansion of others forest formations. This pattern was observed for the two approaches, by using the vegetation map and indicator species.

Key words: Atlantic Forest; Ecological niche models, Climatic fluctuations; Global warming.

Introduction

Past global climate fluctuations played a crucial role in determining the distribution of plant species and entire ecosystems by shifting their limits. Glaciation cycles promoted expansion and retraction of species geographic ranges, thus changing the distribution of vegetation types around the world (Brown and Ab'Saber 1979). Previous studies showed that climate fluctuations were an important driver of current species distribution, with evidence already supported for plants (Svenning and Skov 2007, Dullinger et al. 2012a, Kubota et al. 2015), reptiles (Araújo et al. 2008), beetles (Hortal et al. 2011), and mammals (Li et al. 2015). Concerning vegetation types, the Amazon basin region experienced significant changes in forest-savanna boundaries during the Last Glacial Maximum (LGM) and savannas seem to have expanded only in the early-mid Holocene (Mayle et al. 2004, Anhuf et al. 2006). In European Alps, recent paleoecological studies have shown that climate fluctuations played an important role in treeline ecotone dynamics (Schwörer et al. 2014). Such studies of past climate changes has become an important tool to understand and predict shifts in species and vegetation distribution that might result from global warming (Petit et al. 2008). Understanding the consequences of these distribution shifts to species survival, evolutionary adaptation, ecological interactions, and delivery of ecosystem services could help avoid biodiversity loss by trying to foresee these consequences and developing conservation action targeted to avert them (Moritz and Agudo 2013).

Ecological Niche Models (ENMs) are useful tools to forecast the likely impacts of climate change on species and vegetation types by correlating species occurrence records with current climate to predict future distribution when climate changes (Peterson et al. 2011). Beyond being applied only to species, there are studies using vegetation types or entire biomes to predict shifts in vegetation transitions (Anadón et al. 2014) or to identify areas of historical refugia (Graham et al. 2006, Carnaval and Moritz 2008, Werneck et al. 2011a). Although some authors (e.g. Terribile et al. 2012) claimed that the use of species is more appropriate to develop ENMs than the use of habitat or biome distribution, there are actually no studies integrating the approaches of species with that of vegetation type distribution or proving flaws in the later approach.

Future climatic changes is also a threat to the Brazilian Atlantic Forest biome (AFB), besides deforestation and habitat fragmentation (Joly et al. 2014). The AFB is

considered a Biodiversity Hotspot (Mittermeier et al. 2011), sheltering about 14,000 vascular plants and a large number of endemic species (48% of plant species) (Werneck et al. 2011b), and studies concerning the effects of climate changes on species and ecosystem distribution are a priority research agenda. The AFB is especially understudied in this sense (Souza et al. 2011), but the few studies have found similar consequences to species on a projected future: contraction in the geographic distribution of frogs (Lemes and Loyola 2013, Loyola et al. 2014), trees (Colombo and Joly 2010), birds (Marini et al. 2010, Souza et al. 2011), marsupials (Loyola et al. 2012), and moths (Ferro et al. 2014). Yet, Colombo and Joly (2010) reported a strong tendency for some tree species in shifting their distribution towards southern regions to keep in pace with cooler climate as the temperature increases.

During the LGM, a large stable area of the AFB in the north (known as the Bahia and Pernambuco refuge) was supported, however in the southern Brazil only small patches were predicted to occur (Carnaval and Moritz, 2008). As temperature and humidity have increased, the AFB expanded from the refuges to constitute more continuous forests. Nevertheless, as the AFB is composed by different forest types (seasonal forest, Atlantic rainforest, Araucaria forest) and associated ecosystems (grasslands, and others), one might expect each vegetation type to respond differently to climate change. Environmental factors strongly influence the floristic variation between these forest types, also resulting in different plant community patterns (Marques et al. 2011, Bergamin et al. 2012). Beyond such differences, there are also phylogenetic basis (Duarte et al. 2014), that sustain the classification into a complex of vegetation types. Thus, shifts in temperature and precipitation may influence the vegetation types of the AFB in different ways, being especially susceptible those that occur in colder conditions (Engler et al. 2011), like the altitude grasslands and the Araucaria forest.

The Araucaria forest is characterized by the occurrence of the conspicuous conifer *Araucaria angustifolia* Bertol. (Kuntze) and a mixture of species from different biogeographic origins, such as the Andean and Austral-Antarctic lineages (Duarte et al. 2014). Araucaria forest occurs at latitudes ranging from 18°S to 29.5°S and covers mountainous and plateaus regions, at elevations ranging from 500 to 1.600 meters in the southern and southeastern Brazil (Klein 1960, Jarenkow and Baptista 1987) and in the northeastern Argentina (Misiones Province). However, the *A. angustifolia* occurrence at

31.5°S has expanded the southern limit of Araucaria forest, in the Serra do Sudeste region of Rio Grande do Sul (Carlucci et al. 2011). From the LGM until early to mid-Holocene, when the climate was drier and colder, palynological evidence suggest that grassland vegetation was predominant in the region (Behling 1997, 2002, Ledru et al. 1998, Behling et al. 2004, Jeske-Pieruschka et al. 2010). Nevertheless, in the late Holocene the climate changed to warmer and wetter conditions and the Araucaria forest started to expand from gallery forests and valleys to grassy areas and, in the absence of fire and/or cattle (and grazing livestock), it continues to expand over grasslands under the current climate conditions (Müller et al. 2012). Hence, current distribution of the Araucaria forest is due to past climatic fluctuations, but it might experience a reduction in its geographic distribution as well as species extinction in face of global warming.

To elucidate that hypothesis of limit retraction of the Araucaria forest, here we modeled the spatial distribution of this vegetation type under different climatic scenarios: past climate, during the LGM (*ca.* 21,000 before present) and the Holocene (*ca.* 6000 before present); current climate, and future projections. Our goals were to (1) model the distribution (expansion and retraction) of Araucaria forest during past climatic fluctuations. Although palynological studies have demonstrated the Araucaria forest expansion, there is vast uncertainty of the boundaries of its past distribution because of the limited spatial extent of these studies. ENMs can be a good tool to estimate such boundaries creating a better representation of its earlier distribution; (2) to project the future distribution of Araucaria forest in different scenarios of global warming. Our hypothesis is that the Araucaria forest will suffer a range contraction due to the increase in temperature. Despite the fact that Araucaria forest is still expanding over grasslands (Müller et al. 2012), we expect a replacement of Araucaria forest areas by seasonal forest and Atlantic rainforest in ecotones driven by the increase in temperature (Bergamin et al. 2012); and finally (3) to verify the congruence in projected maps modeled through indicator species occurrence (by using indicator species of the Araucaria forest) (Terribile et al. 2012; Bueno et al. 2016) and through vegetation type, considering the original distribution of the Araucaria forest based on a vegetation map (Carnaval & Moritz 2008; Werneck et al. 2011). There are no studies comparing both approaches, but we expect that indicator species approach will predict larger areas than vegetation map due to the commonly broad distribution range of the species.

Methods

Occurrence data

We used a resolution of 10 arc-minutes (~0.16º x 0.16º grid of latitude and longitude) to model and project the distribution of species or vegetation type across the whole Araucaria forest distribution, encompassing the southern (states of Rio Grande do Sul, Santa Catarina and Paraná) and southeastern (states of São Paulo, Minas Gerais and Rio de Janeiro) regions in Brazil and northeastern of Argentina (the Misiones province). To verify the congruence in the produced maps, we used two sets of data: species data and vegetation type data (i.e. vegetation map).

For the species dataset, we choose 12 species that presented indicator values for the Araucaria forest higher than 0.5 in published papers (Bergamin et al. 2012, Gonçalves and Souza 2014, Oliveira-Filho et al. 2014, dos Santos et al. 2015) that used indicator species analysis (Dufrêne and Legendre 1997) to estimate this value. Beyond the indicator value, another criterion was whether the species occurs only within the distribution of the BAF. Species occurrence records were obtained from the Specieslink (http://splink.cria.org.br) and from a database with species occurrence in the BAF (Bergamin et al. 2015). We used only occurrences records of the southern and southeastern Brazilian region and Misiones, in Argentina.

For the vegetation map dataset, we used Brazil's official vegetation map for the Araucaria forest, which estimates the original distribution before the human occupation (IBGE, 2004). Although the Brazilian official vegetation map does not consider the occurrence of Araucaria forest in the Serra do Sudeste region (Carlucci et al. 2011), we manually included natural Araucaria forest patches of this region in the map.

Climatic data

We modeled the spatial distribution of the Araucaria forest under four scenarios: LGM (21,000 before present), mid-Holocene (6,000 before present), current climate and future projection for 2070 (average for 2061-2080). Future simulations include two representative concentration pathways (RCPs): RCP 2.6 (low emissions scenario) and RCP 8.5 (high emissions scenario). The scenarios were derived from two Atmosphere-Ocean General Circulation Models (AOGCM): CCSM4 and MIROC-ESM. We selected these AOGCM due to availability information for all scenarios. Six climate variables

were downloaded from AOGCM outputs: annual mean temperature, temperature seasonality (standard deviation*100), minimum temperature of coldest month, annual precipitation, precipitation seasonality (coefficient of variation), and altitude. We choose these variables since they are pointed as good predictors of species distribution in the Atlantic forest (Oliveira-Filho and Fontes 2000, Bergamin et al. 2012, Oliveira-Filho et al. 2013). We downloaded the climate variables from WorldClim global climate data (http://www.worldclim.org/) considering the same grid used for species occurrence delimitation.

ENM's, ensemble and uncertainty mapping

ENM's were developed using four algorithms of presence and absence data: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Random Forest (RF), and Boosted Regression Trees (BRT) (Peterson et al. 2011). Because absence data are not available for species data, we randomly selected pseudo-absences (the same number of presences).

On the other hand, for vegetation type data we did have presence and absence data because we know where the Araucaria forest occurs and does not occur. We assumed that the co-occurrence of modeled species for each time period represents the probability of the distribution of Araucaria forest in all scenarios. For each algorithm, we split randomly presence and absence data in 75% to training (calibration) and 25% to test (validation) and repeated this process 100 times. So, species and vegetation type frequencies of occurrence in each cell and at each scenario were obtained on 100 occurrence maps. Models were first generated for current climate and then projected to the other scenarios. Models were evaluated through True Skills Statistics (TSS) and models with low performance were eliminated from the ensembles (models with TSS < 0.6) (Allouche et al. 2006). The TSS is a threshold-dependent measure and provides scores between -1 to 1. Values close to 1 indicate models with better performance. This test is appropriate to evaluate predictive accuracy when presence and absence data are used. Finally, we did an ensemble of the resulted models to produce a more robust forecast (Araújo and New 2007). The analyses were done using package '*dismo'* (Hijmans et al. 2015) in R (R Core Team 2013).

Given that uncertainties are associated with ENM's arising from the variety of simulations from AOGCM's and different time periods (past and future) (Terribile et al. 2012), we calculated uncertainties using ANOVA (Diniz-Filho et al. 2009), by using the probability of occurrence of a given species or vegetation in each grid cell. We used the ENM's and AOGCM's as factors nested in time periods (see Terribile et al. (2012) for a review). Predictive maps combining all the factors represent the uncertainty in the distribution range of the Araucaria forest within each time period.

Finally, we overlap the maps produced through the different datasets (species occurrences and vegetation map occurrence) to observe the congruence among them. To do this, we convert the consensus map from continuous outputs to presence/absence map using a frequency of threshold of 0.6. All geographic information system analyses and maps were performed in ArcGIS version 10 (ESRI 2011).

Paleoclimatic modeling validation

Following Carnaval and Moritz (2008) and Werneck et al. (2011), we validated our paleoclimatic niche models by qualitatively comparing the predicted Araucaria forest distribution with palynological data (fossil pollen records). We included sites within the Araucaria forest distribution and outside to its distributional boundaries, e.g. Neotropical Savanna Cerrado, Atlantic and seasonal forest areas (supplementary material, Table S1). Validation comes from two evidences: 1) if the models predicted the occurrence of Araucaria forest and there were pollen records of *A. angustifolia* or of other characteristic genus or species from this formation (e.g. *Drimys, Lamanonia, Mimosa scabrella, Podocarpus,* and *Weinmannia*) in the site; 2) if the models did not predict the occurrence of Araucaria forest and no pollen records of the above-mentioned species was found in the site.

Results

Models developed for species data (12 indicator species) and vegetation type data were considered good according to the evaluation of TSS (Table 1). Based on TSS values, models of vegetation type reached a better performance (0.87) than the average of the 12 species models (0.75). Overall, both approaches over-predicted the occurrence of Araucaria forest for the present when compared with Brazil's official vegetation map (Figure 1). However, while the vegetation map approach over-predicted less and mainly

over the altitudinal grasslands (Figure 1a), the species dataset predictions went beyond the highland region towards to the south, over areas of seasonal forest and grasslands from the Pampa biome (Figure 1b).

Table 1. Evaluation of the model performance by True Skill Statistic (TSS) for both datasets: 12 indicator species and the vegetation map of Araucaria forest.

	Number of records				
	Presence	**Absence**	**Training dataset**	**Test dataset**	**TSS**
Species	-	-	-	-	-
Annona rugulosa	93	93	70	23	0.71
Araucaria angustifolia	147	147	110	37	0.75
Cinnamodendron dinisii	83	83	62	21	0.70
Cinnamomum amoenum	86	86	64	22	0.80
Cryptocaria aschersoniana	195	195	146	49	0.65
Mimosa scabrella	188	188	141	47	0.71
Myrceugenia cucculata	37	37	28	9	0.82
Ocotea porosa	155	155	116	39	0.74
Piptocarpha angustifolia	95	95	71	24	0.77
Solanum compressum	57	57	43	14	0.79
Solanum corymbiflorum	110	110	82	28	0.84
Zanthoxylum kleinii	43	43	32	11	0.77
Vegetation type	562	8310	421	141	0.87

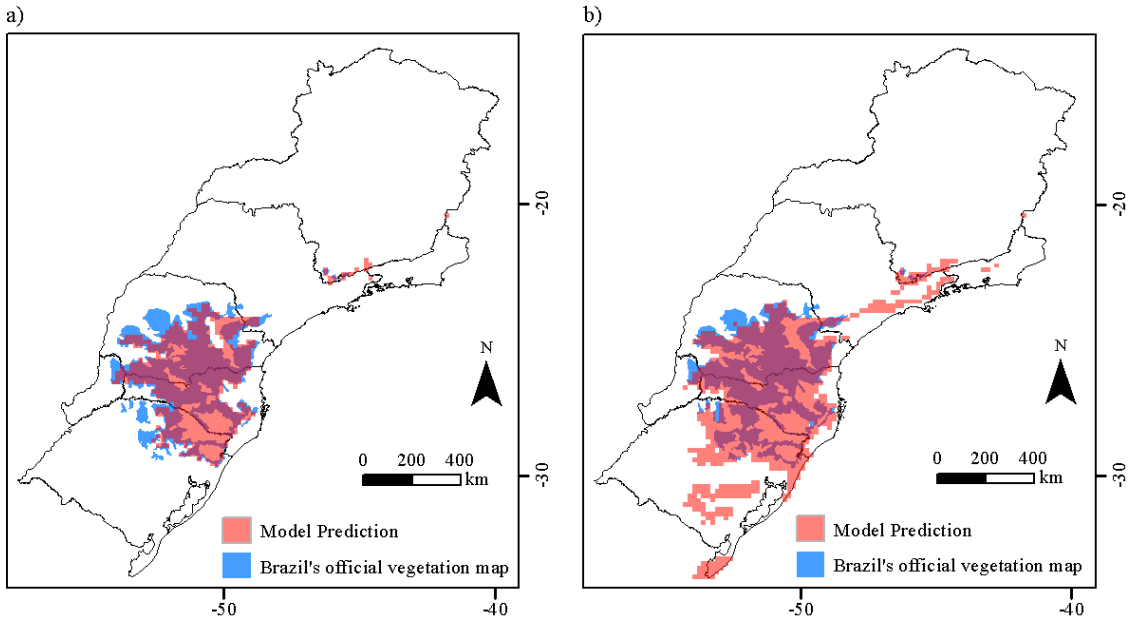

Figure 1. Models of Araucaria forest distribution based on two approaches: (a) from vegetation map model, and (b) from indicator species model both at current climate.

Over the studied time period, models indicated considerable changes in the Araucaria forest distribution for the vegetation type approach (Figure 2) and the species data (Figure 3). Paleomodels suggested a retraction of the Araucaria forest from LGM to mid-Holocene and also, from mid-Holocene to the present (Figure 2a-c and 3a-c). According to these models, the Araucaria forest experienced its higher distribution range during the LGM, when it was spread to north and west, where nowadays these regions shelters Cerrado and seasonal forest, and to the east over the Atlantic rainforest.

Concerning the future predictions, Araucaria forest would suffer a great retraction (Figure 2d-e and 3d-e). The reductions in distribution area were predicted to occur mainly in the western and northern portion of the current forest distribution. It is noteworthy that for the higher greenhouse gas emissions scenario the prediction of retraction was quite dramatic.

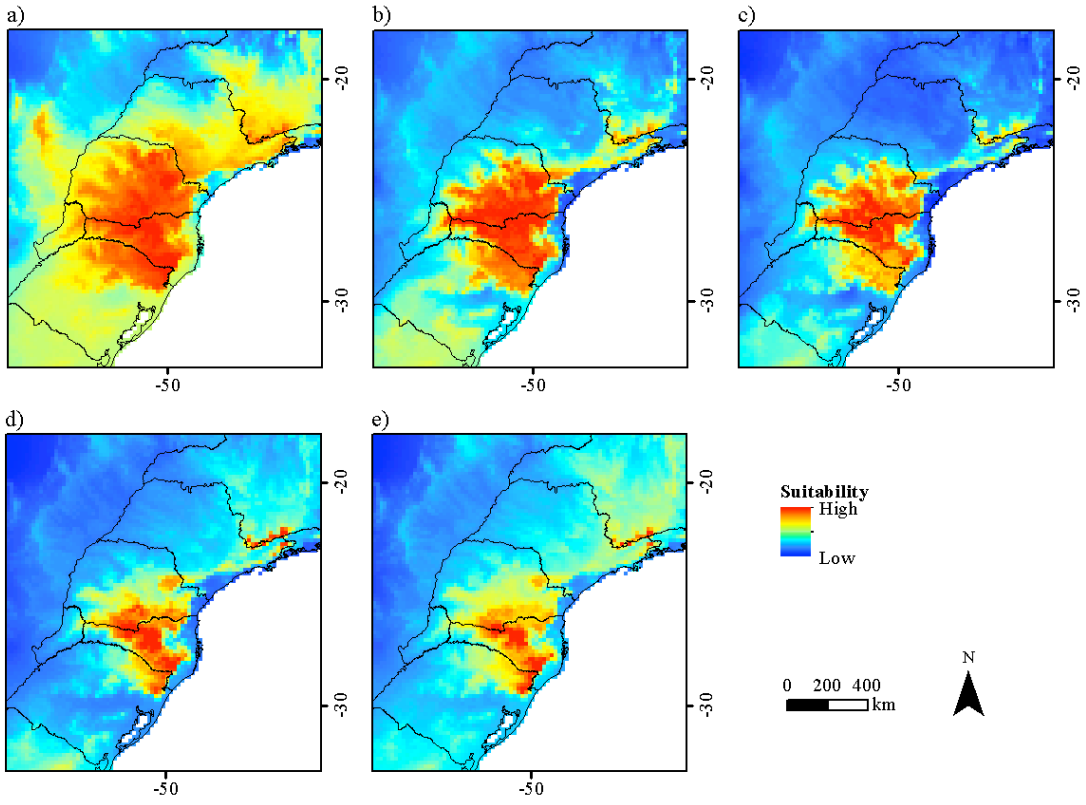

Figure 2. Distribution of Araucaria forest predicted by the vegetation map approach during: A- Last Glacial Maximum (21,000 years before present); B- mid-Holocene (6,000 years before present); C- Current distribution; D- Future distribution (2070) in a low emissions scenario; E- Future distribution (2070) in a high greenhouse gases emissions scenario.

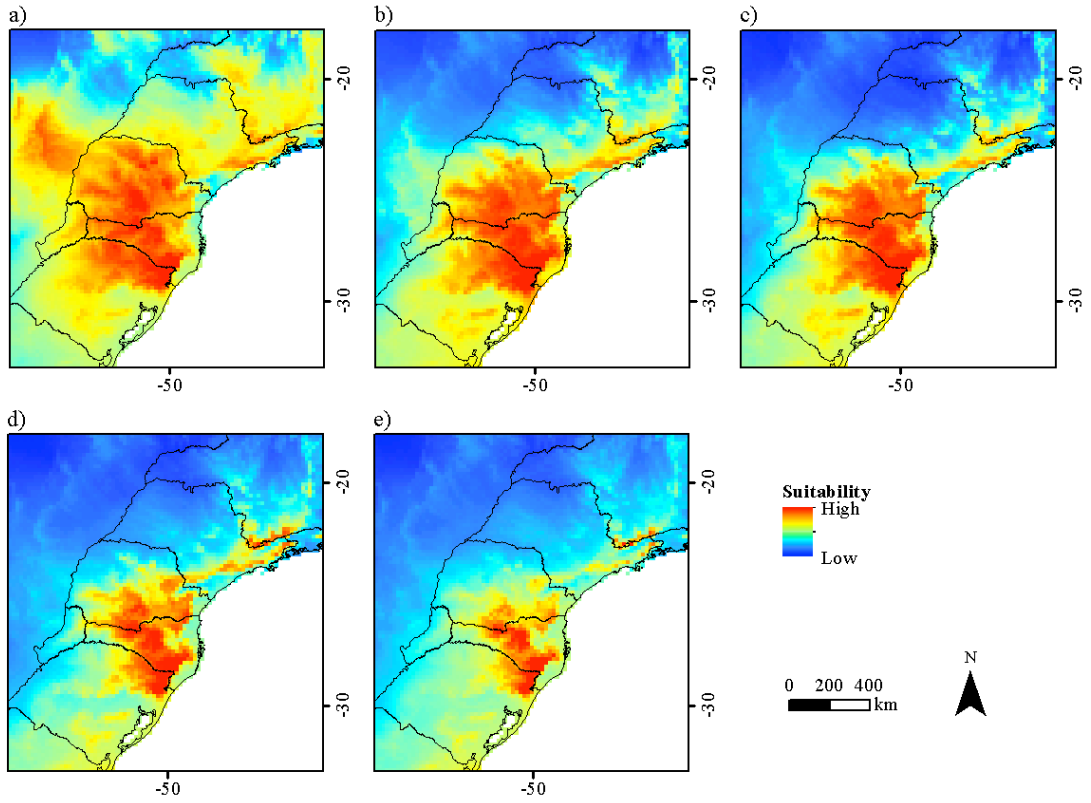

Figure 3. Distribution of Araucaria forest predicted by the species approach during: A- Last Glacial Maximum (21,000 years before present); B- mid-Holocene (6,000 years before present); C- Current distribution; D- Future distribution (2070) in a low emissions scenario; E- Future distribution (2070) in a high greenhouse gases emissions scenario.

The ANOVA indicated that ENMs had the highest mean value and amplitude of uncertainties for the vegetation map approach (Table 2). On the other hand, the time component had the highest mean value and amplitude for the species approach. The AOGCM component had the lowest values for both approaches. Uncertainty distribution varied geographically (supplementary material, Figure S1 and S2). The highest uncertainties values of the ENM are mainly in the north portion for both approaches, however, almost of these values are outside of the current Araucaria forest distribution. For the time component, the highest values inside the Araucaria forest distribution are concentrated in north and west for the vegetation map approach, whereas for the species approach, higher values were almost overall the forest distribution.

Table 2. Mean, minimum and maximum values of uncertainties derived from the nested ANOVA performed for each Araucaria forest grid cell for vegetation map and species approach. Ecological niche model (ENM) and atmosphere-ocean global circulation model (AOGCM) are components of uncertainties and were nested in time.

Data source	Source of uncertainties	Mean(%)	Min-Max (%)
Vegetation map	ENM (time)	46.09	3.80 – 98.08
	AOGCM (time)	5.24	<1 – 61.29
	ENM * AOGCM	2.23	<1 – 18.61
	Time	45	3.78 – 91.78
Species	ENM (time)	37.69	1.48 – 94.87
	AOGCM (time)	10.57	<1- 68.62
	ENM * AOGCM	2.79	<1 – 27.24
	Time	48.94	<1 – 96.80

The paleoclimatic modeling predictions for the LGM and mid-Holocene were largely congruent with the palynological records for both approaches (Figure 4). For the paleoclimatic validation, we had fossil pollen records from 11 localities for the LGM period and from 14 localities for the mid-Holocene period (supplementary material, Table S1). In all localities that the model predicted the occurrence of Araucaria forest, pollen records of *Araucaria angustifolia* or other characteristic genus from this forest formation (e.g. *Drimys, Lamanonia, Podocarpus* or *Weinmannia*) were found. Only two localities where there were pollen records were not included in the predicted occurrence of Araucaria forest by the paleomodels: Ilha do Cardoso (site 13), during the LGM, and Volta Velha (site 6) for the mid-Holocene. These sites presented pollen records of *Drimys* and *Weinmannia*, respectively.

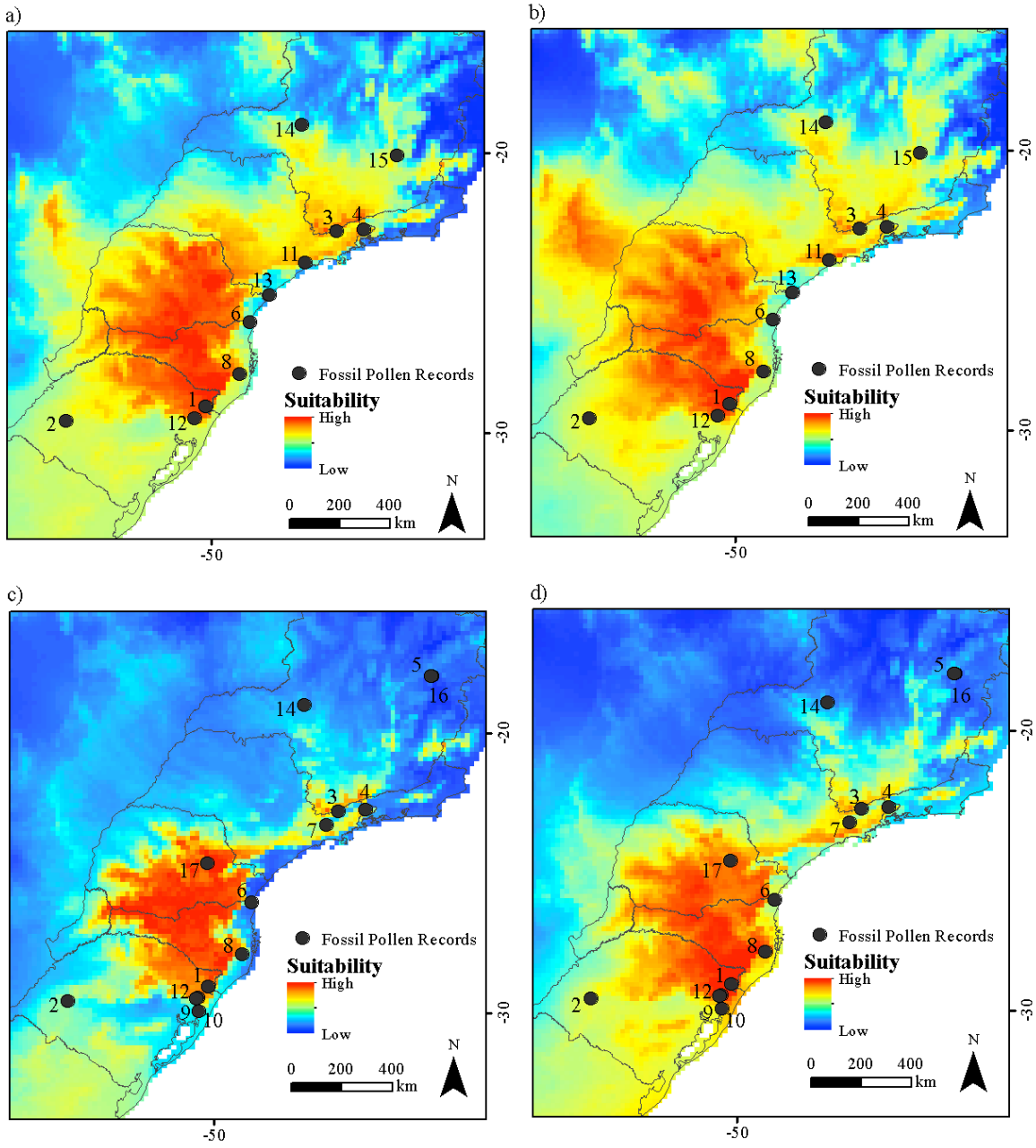

Figure 4. Past predicted distributions of Araucaria forest and the localities with published palynological studies: A- LGM/vegetation approach; B- LGM/species approach; C- mid-Holocene/vegetation approach; D- mid-Holocene/species approach.

Considering the models for the future scenarios, both approaches overall agreed with the retraction of Araucaria forest from LGM. The average congruence of the models generated by species and by vegetation map was 49.60%. Maximum value of congruence was reached in LGM period (61.89%) and minimum value occurred in the future for the high emissions scenario (22.68%). As we expected, species approach always predicted a larger area than the vegetation map approach (Figure 5). In almost all comparisons, vegetation map prediction was inside of species prediction.

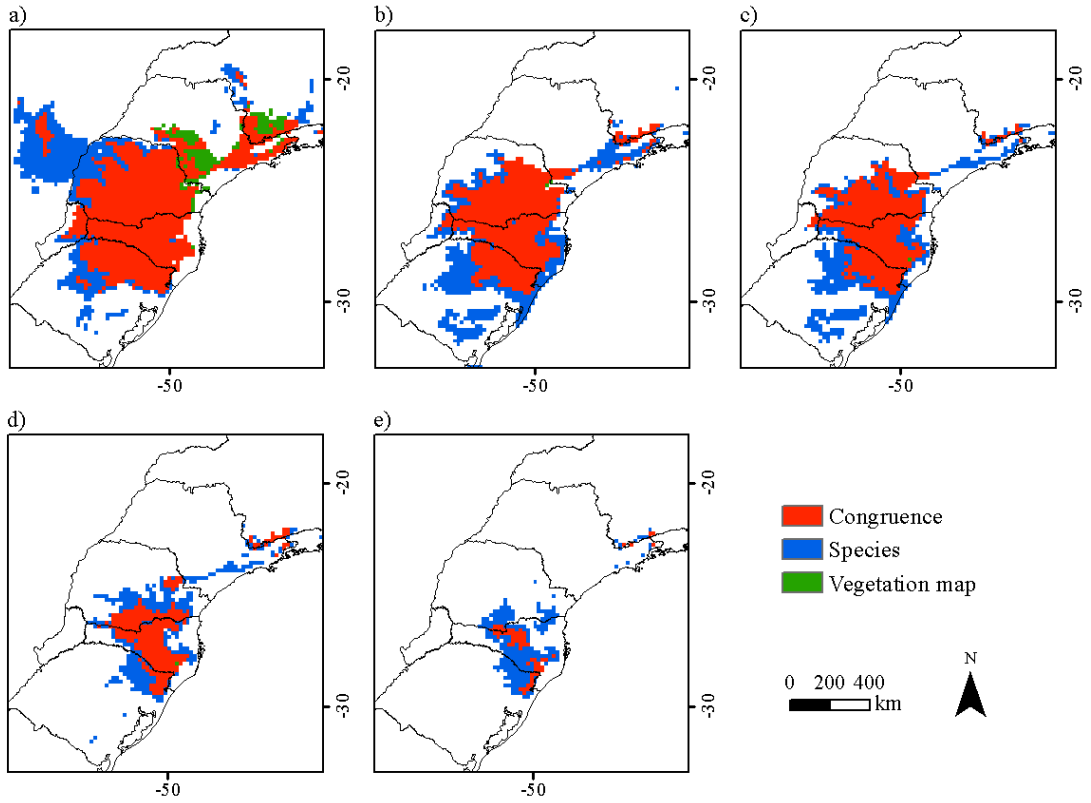

Figure 5. Congruence maps between modeled distributions from vegetation map approach and species approach: A- Last Glacial Maximum (21.000 years before present); B- mid-Holocene (6.000 years before present); C- Current distribution; D- Future distribution (2070) in a low emissions scenario; E- Future distribution (2070) in a high emissions scenario.

Discussion

Our results showed the dynamic of the Araucaria forest during climatic fluctuations. The results allow us to have an understanding about the boundaries of its past distribution, and corroborate our hypothesis that Araucaria forest will likely suffer a great retraction as temperature rise. This pattern is similar to what other studies have found for mountain ecosystems (Nogués-Bravo et al. 2007, Engler et al. 2011). Additionally, there is evidence that the Araucaria forest is suffering a retraction process since from the past and the models for future scenarios indicate a continuously loss in its coverage probably at the expense of the expansion of others forest formations. This pattern was observed for the two approaches, by using the vegetation map and indicator species.

The environmental variables provided important information on the Araucaria forest distribution through the time. The predictions for the current distribution of the Araucaria forest had a good fit, covering almost the entire distribution as indicated by

Brazil's official vegetation map (IBGE, 2004). Despite the overall well fit of the models, some models over-predicted the distribution of the forest on current grassland areas. Many studies have pointed out that current climate conditions favor the expansion of forests over grasslands in the absence of disturbance (e.g. fire and cattle grazing) (Oliveira and Pillar 2004, Duarte et al. 2006, Overbeck et al. 2007, Müller et al. 2012). Fire has been documented since early and mid-Holocene, whereas became more frequent in probably due to the occupation of Amerindians, which may have used the fire for hunting (Behling 1997). Grazing livestock was introduced in the 17th century to this region and today is one of the main economic drivers in the southern Brazilian grasslands. However, this disturbance ensures the biodiversity maintenance, ecological processes of grassland ecosystems (Veldman et al. 2015), and limits the forest expansion. Thus, our models are in accordance with the previous empirical studies, indicating that under current environmental conditions and without disturbances, forests could have already occupied part of the current distribution of grasslands. However, biotic factors such as seed dispersal, colonization, establishment and competition may also interfere in the forest expansion process.

Contrary to our expectation and to the results from palynological studies, our models showed the greatest extent of Araucaria forest distribution during the LGM and then a continuous retraction, mainly in the west portion. Palynological studies have shown the predominance of grasslands during the LGM and suggest that the Araucaria forest was only present in refugia, such as deep and protected valleys and on wetter coastal slopes (Behling 2002; Behling et al. 2004). However, Araucaria forest probably had the maximum expansion towards the north in this period, where nowadays occur the Cerrado and seasonal forest. Pollen records of *Araucaria angustifolia* and other trees such as *Drymis, Clethra, Podocarpus, Weinmannia* and *Mimosa scabrella* were found in peat bogs in these regions (Ledru 1993, Behling and Lichte 1997), corroborating the predictions of our models. These genera are from the temperate flora, characteristics from the Araucaria forest and adapted to cold periods (Rambo 1951, Waechter 2002).

From LGM to mid-Holocene, palynological studies indicated an increase in pollen records of Araucaria forest species, suggesting an expansion of Araucaria forest over grasslands (decrease in grass pollens) mainly due to the increase of temperature (Behling 1998). Conversely, our models predicted a retraction of the Araucaria forest

distribution, especially on the western and northern boundaries. Werneck et al. (2011) found an expansion in the distribution range of the seasonal forest from LGM to Holocene, being the expanded area almost coincident with that of the Araucaria forest retraction. Another important fact is the expansion of the Cerrado vegetation from LGM to mid-Holocene (Bueno et al. 2016). The Cerrado have expanded in the north portion, where our models indicated a retraction of Araucaria forest. The absence of pollen records of Araucaria forest species during the mid-Holocene located in sites inside of the Cerrado reinforces this retraction pattern (Ledru et al. 1993, Behling 1995, 2003). Besides the expansion of seasonal forest and Cerrado, the Atlantic rainforest also seems to have expanded in this period (Carnaval and Moritz 2008). If we consider our models derived from the vegetation map approach, we observed a retraction of the Araucaria forest on the east portion, where the Atlantic rainforest is predominant and have probably expanded. So, despite palynological evidences of an increase of Araucaria forest from the LGM to the mid-Holocene, our models suggest its retraction probably in detriment of the expansion of Cerrado, seasonal forest and Atlantic rainforest. That pollen records increase may have occurred only nearby grassland areas.

Our paleoclimatic models showed that this retraction of the Araucaria forest distribution occurred from the mid-Holocene to the present. Although, some palynological studies, contradictory to ours, have suggested that the warmer and moister climate conditions allowed for a substantial expansion of the Araucaria forest, and not retraction, over grasslands, in addition to an expansion of the Atlantic rainforest from the lowland areas and valleys (Behling 1998, Behling et al. 2007, Jeske-Pieruschka et al. 2013). Such Araucaria forest expansion may have occurred only over plateau grasslands, since our models have shown a contraction in the distribution range throughout the contact zones with seasonal forest (west portion) and Atlantic rainforest (east portion). These forest formations may also have been favored by warmer and moister climate conditions, expanding their range. Current field evidences also suggest that Atlantic rainforest and seasonal forest species are still expanding through the establishment of saplings into the understory of Araucaria forest (Klein 1984, Bergamin et al. 2012).

As already mentioned, the paleoclimatic models were largely congruent with palynological records. Our models match almost all sites with pollen records of *Araucaria angustifolia* or other characteristic species from the Araucaria forest

formation. But, while the palynological studies are in agreement with an expansion of the Araucaria forest from LGM to the present time, our models predicted a retraction in the distribution range. This retraction occurred in the northern portion where the forest probably occurred during the LGM and vanished in the mid-Holocene. Most sites of palynological studies are grouped in eastern Brazilian highlands, which does not allow us to have an idea about the boundaries and the range of the Araucaria forest past distribution, mainly in the west where our models predicted a large suitable area for its occurrence. Nevertheless, the results of the palynological validation were consistent even knowing the limitation of pollen data and the potential pitfalls associated with their use (Carnaval and Moritz 2008).

Regarding the future, model predictions indicate a great contraction in the distribution of the Araucaria forest, as we hypothesized. As the temperature increasing, our models indicate a migration of the Araucaria forest to areas with high altitude, with consequently low temperatures and frost events in the winter, to keep pace with climate changes. The coexistence of elements from Andean and Austral-Antartic flora (Rambo 1951, 1953, Gonçalves and Souza 2014) characterizes the species composition of the Araucaria forest as cold-adapted. On the other hand, low temperatures and frost may be an important abiotic filter to limit the expansion of the tropical flora of the Atlantic rainforest and seasonal forest. Both forests will probably expand their distribution with the increasing temperatures, strangling the Araucaria forest. Global warming has been indicated as one of the major threats to mountain ecosystems (Nogués-Bravo et al. 2007, Engler et al. 2011). The effects on plants occur mainly due to an upward shift in the distribution and has already been detected in many parts of the world (Kelly and Goulden 2008, Lenoir et al. 2009, Feeley et al. 2011). Mountain species are more sensitive and threatened by climate changes because they have less opportunity for upward migration, leading them to mountain-top extinctions in extreme cases (Dullinger et al. 2012b). As the distribution of the Araucaria forest already occurs in upper parts of mountains, especially in southeastern region (Hueck 1972), many species may be at extinction risk in the future, mainly in the higher emission of greenhouse gas scenario.

Both modeling approaches agreed with the contraction of Araucaria forest from LGM to future scenarios. However, the vegetation map approach produced more restrictive/conservative predictive models whereas the species approach always

predicted larger suitable areas. The choice of the species certainly affects the models result. The use of indicator species, which method considers the frequency and abundance of species in different habitats (Dufrene and Legendre 1997), to choose the group of species should decrease the overestimation of suitable maps. However, even an indicator species may have a broad distribution range (Bueno et al. 2016), influencing the model performance and generating maps with large suitability areas due to the variety of environmental conditions that the species can occur. On the other hand, the vegetation map database is defined on a group of species (which can be coincident with the indicator species) that characterize a vegetation formation in a certain predominant climate (IBGE, 2015). Thus, without great climatic variability, predictive models tend to be more restrictive/conservative. In addition, the vegetation map approach may decrease biases derived from presence/absence species data.

Conclusions

The paleomodels showed a retraction of the Araucaria forest since the LGM to the present time. Yet, paleomodels also indicated that Araucaria forest had the widest expansion during the LGM, in a colder climate conditions. It is noteworthy that we are not asserting that Araucaria forest occurred in the entire distribution range as predicted by paleomodels, but that the climate would be suitable to that occurrence. According to our results, at the same time that the Araucaria forest seems to have expanded over grasslands, as evidenced by palynological studies, occurred a larger retraction in contact zones with seasonal forest and Atlantic rainforest under warmer climate. Future predictions further indicated a great retraction of the Araucaria forest, mainly for the high emission greenhouse gas scenario, where the temperature is expected to increase 3.7°C in average (2.6°C - 4.8°C). High altitudinal areas where the temperatures will be milder may be potential refuges for the Araucaria forest in the future. But today most of these areas shelter high diversity grasslands with cattle grazing and fire disturbances, which in turn prevent the Araucaria forest expansion. In addition, it is important to highlight that our models did not consider anthropogenic factors, as habitat loss, land use and fragmentation, but only climatic variables. By considering anthropogenic factors, the predictions could be much worse for the future. Finally, further studies are necessary to understand the complex dynamic of Araucaria forest and grasslands mosaics to design conservation planning, as both vegetation types are threat by climate changes.

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CAPÍTULO 4

Contrasting responses of tree species in face of climate change in Atlantic Forest ecotones: migrations trends and short-term dynamics[#]

Rodrigo S. Bergamin [a,b], Vinícius A.G. Bastazini [c], Alexander Vibrans [d], Rafael D. Loyola [b,e], Sandra C. Müller [a]

[a] Laboratório de Ecologia Vegetal, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil;

[b] Laboratório de Biogeografia da Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, Goiás, Brazil;

[c] Centre for Biodiversity Theory and Modeling, Station D'Ecologie Experimentale du CNRS, Moulis, France;

[d] Inventário Florístico Florestal de Santa Catarina, Departamento de Engenhaia Florestal, Universidade Regional de Blumenau, Bumenau, Santa Catarina, Brazil;

[e] Centro Nacional de Conservação da Flora, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil.

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Abstract

Climate change is expected to drive important changes in trees species distribution. So, trees species must shift their ranges to higher latitudes or elevations to keep in pace with global warming. Predicting species responses is a major challenge in order to create efficient strategies to minimize and mitigate their effects. Using two different dataset from permanent plots, we investigate how tree species are responding to climate change effects in Atlantic Forest ecotones. With the first dataset, we show migrations trends (upward and downward) between saplings and adult tree species due to global warming in an altitudinal gradient in the Atlantic Rainforest ecotones. With the second dataset, we evaluate short-term changes in different strata of plant species through time dividing them into different groups of tropical, temperate and generalist species in ecotone areas of Araucaria Forest and Atlantic Rainforest. Our results suggest an unexpected migration trend, where 66% of the species showed a downward shift of their center of gravity. Regarding to short-term changes, temperate species exhibited the worse performance in almost all strata whereas the tropical group showed an opposite pattern. Species are responding idiosyncratically to the ongoing temperature increase. Species that occurs in higher altitudes are being more affected and as consequence, they have to shift their distribution towards colder areas to remain within their thermal niches. However, species depend on the availability of new areas to colonize. Temperate species are occurring in the end of the altitudinal gradient and probably would have nowhere to migrate. It is important to continue monitoring these ecotonal areas in the Atlantic Forest with permanent plots in order to understand the consequences climate change and mitigate its effect on this biodiversity hotspot.

Key words: Atlantic Rainforest; Araucaria Forest; Upward; Downward; Tropical species; Temperate species.

Introduction

Understanding how global climate change impact natural ecosystems is considered one of the most urgent challenges faced by scientists in order to create efficient strategies to minimize and mitigate their effects (Tylianakis et al. 2008, Gilman et al. 2010, Bellard et al. 2012). Climate change will affect processes and patterns of species, biotic interactions and food webs by altering dispersal rates, creating spatial and temporal decoupling of ecological interactions and promoting shifts in the geographic distributions of organisms that may result a reorganization of communities and biotic interactions (Thomas 2004, Loarie et al. 2009, Bellard et al. 2012, Ferrarini 2013). Changes in species distribution have important implications for their conservation, potentially leading to extinctions due to reductions in habitat area and quality or in population size, and to local declines in biodiversity because of "biotic attrition" (Colwell et al. 2008). Many shifts in species distribution associated to climate changes have been observed worldwide (Thuiller et al. 2005). The evidences suggest that many species of several taxonomic groups are migrating to colder areas towards the poles (higher latitudes) or to higher altitudes in mountainous regions (upslope of lowland species) (Hickling et al. 2006, Feeley et al. 2011).

Climatic fluctuations strongly influence the distribution of vegetation around the world, resulting in expansion and retraction of distinct vegetation types especially in ecotone zones – transitional areas between two contrasting communities or ecosystems (Delcourt and Delcourt 1991). Ecotone zones are highly diverse, as relative sharp environmental gradients can shelter the co-occurrence of many species from different ecosystems (Smith et al. 2001). Ecotones are even considered to be highly sensitive to climate change, because they are justly located at sharp transitions where the boundaries of species range distribution are often climatically controlled (Solomon 1986, Noble 1993, Myster 2012). Thus ecotones are important systems for detecting early signs of climate-induced changes (Solomon 1986, Noble 1993), such as in contrasting physiognomies of grassland-forest ecotones (Myster 2012) and coastal zones (Jiang et al. 2016). However, in many situations ecotones occur between more discrete plant physiognomies, such as along distinct forest formations within a region.

Ecological niche models provide a good tool to forecast the potential effects of climate change on species range and vegetation transition in ecotone areas in a broad scale. However, there is few empirical data to support model predictions to provide

more accurate species and vegetation responses at local and regional scales (Zhu et al. 2012). Historical data from permanent plots have been used to show that as temperature rise, species are shifting their distributions to keep in pace with climate change. Especially in the in European Alps, many studies that resampled data of plant species indicated an upward shift in the treeline ecotone (Pauli et al. 2007, Gottfried et al. 2012). Resampling data over time can provide a more accurate projection on how climate will affect species demography into the future (Dolanc et al. 2013). Despite the importance of resampling data from permanent plots to project future changes in biodiversity, long-term studies in Brazil are still in the beginning (Malhi et al. 2002).

The Brazilian Atlantic Forest encompasses different forest physiognomic types and associated ecosystems (e.g. grasslands, coastal scrublands), with heterogeneous environments (Oliveira-Filho and Fontes 2000) and high levels of beta-diversity (Bergamin et al. 2017). With a remarkable range of altitudinal (from sea level up to 2700 meters) and latitudinal gradients (5º N to 33° S), the Atlantic Forest constitutes an important scenario for studies on the effects of climate change on the distribution of species and vegetation types, especially in ecotone zones. The current distribution of the Atlantic Forest is due to past climatic fluctuations (Behling et al. 2004, Carnaval and Moritz 2008, Werneck et al. 2011), which led to the expansion and retraction of distinct vegetation types. Several studies indicate that after the last glaciation, current climate conditions, mainly the increased humidity and temperature, have favored forests expansion over ancient grasslands (Behling et al. 2004, Oliveira and Pillar 2004) and also the immigration of tropical species (from Seasonal Forest and Atlantic Rainforest of lower altitudes) into the understory of the Araucaria Forest (Bergamin et al. 2012). Thus, global warming has been pointed out as the main cause of processes of forest expansion over grasslands and also the upslope migration of species typically from lower altitudes toward higher altitudes.

In this paper, we investigate how tree species are responding to climate change effects in permanent plots located in Atlantic Forest ecotones. We illustrate our perspectives using two datasets from southern Brazil. The first is the dataset from permanent plots of the Forest Floristic Inventory of Santa Catarina (Vibrans et al. 2010). We show migration trends comparing juvenile and adult tree species in an altitudinal gradient (2-1160 m) of the Atlantic Rainforest. Our main goal here is to indicate which species are probably shifting its distribution and in which direction (upward or downward) along ecotonal zones. The second dataset comes from permanent plots of

the Long Term Ecological Research Program in the Southern Atlantic Forest. We evaluate short-term changes (six years period) in species composition due to stem growth, mortality and recruitment in ecotone areas of Araucaria Forest and Atlantic Rainforest. Our main goal is to analyze the performance of plant species through time, but considering the species within groups according to their climate affinity: tropical, temperate and generalist species.

Methods

Study area

The permanent plots are located in the Southern Atlantic Forest in Santa Catarina and Rio Grande do Sul states. Permanent plots in Santa Catarina (www.iff.sc.gov.br) ranges from 2 to 1160 meters of altitude and encompasses ecotone zones from lowland Atlantic Rainforest and highland Araucaria Forest, which generate turnover in plant species composition (Bergamin et al. 2012, 2017). On the other hand, permanent plots in Rio Grande do Sul (Bergamin 2010) are located in Araucaria forests in the eastern plateau border with 900 meters of altitude in average. Natural vegetation contains ecotone zones of Araucaria Forest and grasslands in the plateau and between montane Atlantic Rainforest in the slopes.

Data from Forest-Floristic Inventory of Santa Catarina and migration trend analysis

As long-term data from permanent plots resampling are not yet available, we use a "life stage for time" substitution to infer about plant species migration (upward or downward). Juveniles are used as proxy of recent climatic conditions and adults reflects a response to former conditions (Lenoir et al. 2009, Zhu et al. 2014, Serra-Diaz et al. 2015). We selected juveniles (0.5 m to 2 m tall) and adults tree species (≥ 10 cm of diameter at breast height [DBH]) sampled in the same plots along the altitudinal gradient (Vibrans et al. 2010). We excluded tree species that does not occurred in at least three plots and with less than 10 individuals in overall. We also excluded plots that were not classified as mature forest stands to avoid differences between the two strata from secondary succession dynamics. Thus, we finally stand with 103 permanent plots and 159 tree species that occur in both life stages (juvenile and adult).

Following Chen et al. (2009) and Feeley et al. (2011), we calculated the center of the elevation distribution (or center of gravity) for each species as the mean elevation weighted by the number of individuals per elevation level. We did this for all species

into each life stage, i.e. each species had a center of gravity as juvenile and another as adult. Thus, we tested for changes in the mean elevation for all the 159 species considering their values in both life stages. If the center of gravity for juveniles is higher than for adults, we infer an upward migration, while the opposite is associated to a downward migration. We also test for directional changes in the floristic composition for each plot calculating the community elevation score (CES) (Chen et al. 2009, Feeley et al. 2011). The CES is the mean centre of gravity of all species sampled in the plot (including those species that were excluded due to small number of individuals and frequency in the plots) based on the values from adults (since they represent former conditions) and weighted by species abundances in the plots. The weighting procedure considered either the sample of adults and of juveniles. Then, we obtained a deviation value by subtracting the juvenile's CES by the adult's CES. Therefore, negative values indicate an increase in the abundance of species from lower elevations while positive values indicates an increase in the abundance of species from higher elevations. However, to standardize with the pattern of species level migration, we showed our CES result as positive values to indicate upslope migration.

Data from Long Term Ecological Research Program in the Southern Atlantic Forest and short-term change analysis

Data from nine permanent plots resampled after six years (2009-2015) were used to infer short-term changes in floristic composition and forest structure (for more details about sample methodology please see Bergamin 2010). Resampled data comes from three different strata of the forest: lower stratum (seedlings with 0.3 m of height to 0.99 cm of DBH), intermediate stratum (saplings with 1 to 4.9 cm of DBH) and upper stratum (trees with ≥ 5 cm of DBH).

We evaluate the performance of plant species after six years of the first survey. The performance of species was defined as demographic changes in abundance and basal area through time. We calculated the variation of species abundance using the formula $\Delta A_i = \ln(Nt_2) - \ln(Nt_1)/t$ (where N is the number of individuals of species *i*, t_1 and t_2 are, respectively, the first and the second survey, and t is the time interval in years) and variation in basal area using the formula $\Delta BA_i = \ln(Bat_2) - \ln(Bat_1)/t$ (where Ba (m^2) is the sum of stem basal area of species *i* in t_1 and t_2 respectively). Thus, positive values represent gain of individuals and in basal area. We performed the

calculations for all strata, however, for the seedlings we did not calculate the variation in basal area because we just have the number of individuals.

The species were then classified into different groups: tropical, temperate and generalist species. The tropical group should represent species from the Atlantic Rainforest that are migrating (probably due to increasing temperatures) into the Araucaria Forest, while the temperate group represents cold-adapted species from the Araucaria Forest, and the generalist group the species that are indifferent to these both forest types. To classify the species into the groups, we performed a classification method to determine habitat specialists and generalists (Chazdon et al. 2011; see the supplementary material for details about this method) with a broad data set of surveys from Araucaria Forest and Atlantic Rainforest of southern Brazil. We then performed variance analysis (ANOVA) through randomization test with 10,000 permutations to evaluate the differences between species groups in terms of abundance and basal area variation (ΔA and ΔBA). The ANOVA was performed with the software Multiv (Pillar 1997), available in http://ecoqua.ecologia.ufrgs.br.

Results

Migration trends

Overall, most of species showed downward migration trends. From the 159 species selected, 105 had the center of gravity for adult trees higher than for juveniles (Table 1). The other 54 species showed an upward migration trend. However, the results of CES demonstrated a different pattern. Fifty percent of the community plots (52 of 103) presented a higher CES for juveniles than adults (Figure 1). Most of these communities are located above 400 meters of altitude in the studied gradient, indicating an upward migration trend when considering their overall community composition. Yet, most of communities located below 400 meters of altitude showed a downward migration pattern.

Table 1: Center of gravity of juvenile and adult tree species with the lower and upper limits of occurrence in the studied altitudinal gradient.

	Center of Gravity		Juvenile		Adult trees	
Species	Juvenile (m)	Adult trees (m)	Lower limit (m)	Upper limit (m)	Lower limit (m)	Upper limit (m)
Actinostemon concolor	310.67	317.75	50	821	18	842
Aiouea saligna	283.20	308.98	2	708	2	874
Alchornea triplinervia	418.58	586.61	2	1160	2	1160

Allophylus edulis	265.33	454.23	2	857	89	928
Allophylus petiolulatus	244.55	260.54	105	442	97	803
Alsophila setosa	560.35	648.30	106	914	60	928
Amaioua guianensis	278.06	283.10	2	718	2	803
Andira fraxinifolia	157.32	126.56	2	611	2	588
Aniba firmula	397.11	386.40	2	835	2	842
Annona emarginata	493.85	525.03	231	914	251	928
Aparisthmium cordatum	218.12	220.21	2	357	2	803
Aspidosperma australe	504.77	581.70	34	928	5	928
Aspidosperma parvifolium	774.07	605.18	525	806	458	708
Bathysa australis	523.87	486.89	18	841	34	841
Brosimum lactescens	217.00	255.06	18	640	34	803
Byrsonima ligustrifolia	580.50	606.01	14	857	2	938
Cabralea canjerana	450.79	488.28	5	1160	14	1160
Calophyllum brasiliense	9.49	7.30	2	114	2	14
Calyptranthes grandifolia	533.53	563.73	60	1160	97	874
Calyptranthes lucida	291.82	249.53	18	1160	5	1160
Calyptranthes strigipes	225.22	317.58	18	639	5	803
Campomanesia xanthocarpa	377.39	410.54	226	733	105	765
Casearia decandra	497.95	698.70	246	857	226	914
Casearia obliqua	384.86	432.69	89	808	89	857
Casearia sylvestris	471.71	369.73	18	914	34	928
Cecropia glaziovii	274.00	332.18	8	821	14	823
Cedrela fissilis	369.71	468.42	89	821	34	938
Chrysophyllum inornatum	173.31	387.33	50	311	50	765
Cinnamomum glaziovii	719.56	505.89	458	972	105	928
Citronella paniculata	548.93	675.97	246	928	276	928
Clethra scabra	456.37	437.24	18	821	2	842
Clusia criuva	343.12	427.93	8	718	2	874
Coccoloba warmingii	672.20	605.84	34	914	5	914
Copaifera trapezifolia	530.43	515.55	106	823	18	803
Cordia trichotoma	1057.12	378.39	226	1160	192	733
Cordiera concolor	593.25	656.71	14	1160	50	938
Coussarea contracta	649.41	655.03	65	972	64	938
Cryptocarya aschersoniana	706.45	628.86	154	972	5	874
Cryptocarya mandioccana	520.52	565.73	106	938	5	938
Cupania vernalis	441.46	457.92	65	1160	14	1160
Cyathea corcovadensis	308.02	344.01	60	786	5	745
Cyathea delgadii	291.18	567.05	256	351	34	938
Cyathea phalerata	592.79	693.85	8	972	8	1160
Duguetia lanceolata	447.93	377.10	50	747	50	747
Endlicheria paniculata	514.50	350.12	2	972	124	611

Esenbeckia grandiflora	415.40	614.62	5	972	5	938
Eugenia handroana	424.63	524.20	18	972	5	914
Eugenia involucrata	614.79	520.33	311	806	215	874
Eugenia melanogyna	496.40	525.17	34	698	97	759
Eugenia multicostata	328.63	377.15	50	585	50	744
Eugenia rostrifolia	310.65	590.89	270	345	270	765
Eugenia stigmatosa	351.74	161.69	18	806	18	708
Eugenia ternatifolia	524.31	470.54	89	823	18	841
Eugenia verticillata	414.60	524.44	192	747	192	759
Euterpe edulis	274.90	290.96	2	914	34	914
Faramea montevidensis	350.19	196.21	50	640	5	803
Garcinia gardneriana	261.98	233.52	2	643	2	803
Guapira opposita	369.05	432.62	2	874	5	938
Guarea macrophylla	187.59	424.05	2	823	5	759
Guatteria australis	482.43	622.13	2	972	8	938
Hedyosmum brasiliense	191.28	211.00	2	294	8	803
Heisteria silvianii	343.78	307.56	18	733	5	803
Hieronyma alchorneoides	289.96	671.08	5	479	311	765
Hirtella hebeclada	334.89	339.89	8	643	5	803
Ilex brevicuspis	397.18	432.17	60	808	60	1160
Ilex microdonta	205.08	637.68	2	718	89	1160
Ilex theezans	544.50	538.44	5	821	5	1160
Inga marginata	340.02	371.96	18	914	18	823
Inga sellowiana	340.10	265.47	18	639	34	803
Inga sessilis	683.72	562.05	260	972	34	914
Inga vera	352.50	113.43	18	639	18	345
Jacaranda micrantha	177.83	342.00	89	786	5	914
Jacaranda puberula	476.50	442.99	8	806	5	857
Laplacea fructicosa	656.50	800.38	18	821	154	1160
Machaerium stipitatum	521.29	416.70	226	857	89	857
Magnolia ovata	331.35	323.61	50	601	5	842
Marlierea eugeniopsoides	327.38	308.82	2	793	14	823
Marlierea excoriata	473.69	511.76	18	972	206	808
Marlierea obscura	122.15	239.53	5	611	5	765
Marlierea silvatica	310.16	728.35	97	744	245	823
Marlierea tomentosa	233.43	261.14	5	718	5	708
Matayba intermedia	364.48	412.03	2	972	2	938
Maytenus robusta	473.07	573.92	2	938	5	938
Meliosma sellowii	359.27	447.30	18	708	50	928
Miconia budlejoides	339.43	359.58	97	718	97	803
Miconia cabucu	346.45	406.11	18	793	5	914
Miconia cinnamomifolia	182.16	277.80	8	453	18	803
Miconia cubatanensis	539.02	386.43	5	841	2	874
Mollinedia clavigera	515.03	680.63	106	972	206	928
Mollinedia schottiana	461.57	664.31	14	972	323	842

Mollinedia triflora	594.50	522.13	60	972	226	841
Myrceugenia myrcioides	657.27	672.08	105	1160	8	938
Myrcia aethusa	364.18	321.22	50	1160	18	744
Myrcia brasiliensis	622.38	367.24	2	972	2	914
Myrcia glabra	409.42	347.00	18	808	5	808
Myrcia guianensis	413.53	666.64	154	1160	18	1160
Myrcia hebepetala	453.67	648.04	65	1160	64	1160
Myrcia pubipetala	508.47	478.33	89	928	5	874
Myrcia pulchra	653.83	561.43	294	1160	5	874
Myrcia spectabilis	305.63	315.95	18	914	60	803
Myrcia splendens	476.39	502.07	18	857	34	938
Myrcia tijucensis	371.08	378.47	18	1160	34	928
Myrciaria floribunda	352.13	491.65	50	718	5	857
Myrocarpus frondosus	434.69	421.74	124	808	18	823
Myrsine coriacea	358.44	356.46	124	938	8	857
Myrsine lancifolia	660.75	698.48	258	821	525	874
Myrsine umbellata	476.51	565.47	2	938	2	1160
Nectandra megapotamica	428.23	448.17	89	835	186	928
Nectandra membranacea	260.00	275.07	34	555	18	835
Nectandra oppositifolia	412.05	374.84	50	972	5	914
Neomitranthes glomerata	180.34	255.82	2	744	5	803
Ocotea aciphylla	346.96	336.25	2	643	2	803
Ocotea catharinensis	741.58	629.45	106	972	50	938
Ocotea corymbosa	415.52	684.30	329	835	97	1160
Ocotea dispersa	198.50	128.35	5	453	5	453
Ocotea elegans	506.83	623.19	34	1160	18	1160
Ocotea glaziovii	798.62	651.38	698	972	97	841
Ocotea odorifera	542.55	641.64	114	972	14	938
Ocotea pulchella	21.80	177.29	2	60	2	1160
Ocotea pulchra	550.77	571.34	14	803	5	874
Ocotea silvestris	588.81	522.74	89	841	5	928
Ormosia arborea	509.67	621.15	5	914	5	938
Ouratea parviflora	436.27	655.86	2	972	294	938
Ouratea vaccinioides	553.54	571.72	294	874	294	914
Pachystroma longifolium	310.72	230.40	124	555	60	345
Pausandra morisiana	189.67	207.71	34	744	18	640
Pera glabrata	149.13	304.92	2	821	2	857
Piptadenia gonoacantha	151.90	172.21	89	307	89	540
Piptocarpha axillaris	764.75	513.08	215	938	64	938
Pisonia ambigua	330.00	363.45	34	744	60	744
Platymiscium floribundum	338.00	323.34	106	808	2	803
Podocarpus sellowii	712.20	550.47	5	1160	258	1160

Posoqueria latifolia	493.40	606.85	8	972	89	938
Protium kleinii	309.89	320.67	50	623	5	803
Prunus myrtifolia	547.11	555.22	34	1160	89	1160
Pseudobombax grandiflorum	443.25	418.41	311	479	60	841
Psidium cattleianum	236.81	293.97	8	835	5	841
Psychotria carthagenensis	246.19	253.49	89	351	18	803
Psychotria suterella	534.09	559.76	14	972	97	803
Psychotria vellosiana	476.98	643.71	50	972	60	938
Quiina glazovii	244.94	298.97	34	634	105	634
Roupala montana	375.58	496.28	89	938	89	938
Rudgea jasminoides	404.34	594.32	50	972	60	841
Schefflera angustissima	189.63	588.12	2	928	2	938
Sloanea guianensis	223.00	296.17	14	525	5	808
Sorocea bonplandii	377.59	404.90	50	914	50	938
Stylogyne pauciflora	528.43	343.61	34	823	14	453
Syagrus romanzoffiana	330.60	264.28	8	714	2	842
Symplocos tenuifolia	273.07	714.67	18	590	215	874
Tapirira guianensis	82.00	134.08	2	453	2	803
Tetrorchidium rubrivenium	361.64	340.33	114	733	60	786
Trema micrantha	439.08	477.26	256	733	60	928
Trichilia clausseni	386.34	374.13	246	555	246	765
Trichilia lepidota	259.52	293.14	50	835	50	841
Vantanea compacta	385.58	336.57	220	623	97	623
Virola bicuhyba	211.06	271.51	18	640	18	842
Xylopia brasiliensis	236.89	285.64	18	640	5	803
Zanthoxylum rhoifolium	371.41	377.68	50	808	34	874
Zollernia ilicifolia	354.85	438.76	60	972	64	792

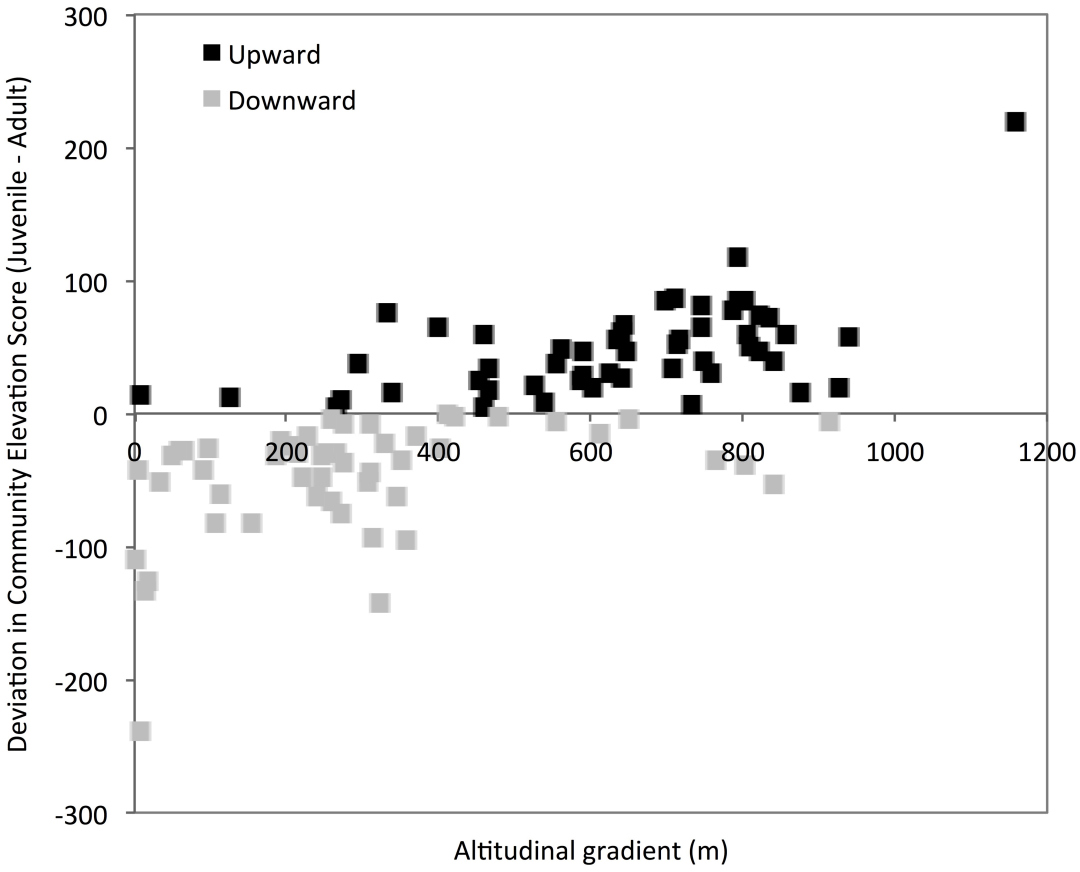

Figure 1: Deviation results (juvenile – adult) of the community elevation scores (CES) for each community plot. Black squares represent upward migration and gray squares represent downward migration.

Short-term changes

Twenty-seven species were classified as generalists, 13 as temperate, and 13 as tropical (supplementary material Table S1). Twenty-six species were too rare to be classified and 25 species were not possible to classify in any group due to lack of information. In the lower stratum, the generalist group showed a positive balance in abundance (i.e. more recruitment than mortality of individuals), differing from the groups tropical and temperate ($p < 0.05$), which presented an opposite pattern (Table 2). For the intermediate stratum, the tropical group demonstrated a positive balance in abundance when compared with the other two groups, however differences were significant only in the comparison to the temperate group. Moreover, generalists and tropical species had a significant increase in basal area when compared to the temperate group. In the upper stratum, any significant difference for abundance was observed, but the tropical group presented significant higher values in basal area than the other two groups (Table 2).

Table 2: Average values of short-term variance in abundance (ΔA) and basal area (ΔBA) of species according to the groups (generalist, temperate and tropical) for each forest stratum. Different letters indicate significant differences ($p < 0.05$) between groups.

	Δ Abundance	Δ Basal Area
Lower stratum		
Generalist	0.028 [a]	
Temperate	-0.097 [b]	
Tropical	-0.031 [a]	
Intermediate stratum		
Generalist	-0.015 [ab]	0.044 [a]
Temperate	-0.044 [b]	-0.041 [b]
Tropical	0.002 [a]	0.102 [a]
Upper stratum		
Generalist	-0.028 [a]	0.023 [a]
Temperate	0.013 [a]	0.035 [a]
Tropical	0.014 [a]	0.124 [b]

Discussion

Community and species distribution patterns along an altitudinal gradient, as well as short-term dynamics of distinct groups of species in ecotonal zones of the Atlantic Forest in southern Brazil are evidencing consistent changes that may are associated to climate warming. We observed both upward and downward migration patterns at the species level, but by analyzing the community elevation score, which is weighted by species abundance, a clear upward migration was identified for sites located above 400 m of altitude. Yet, we verified that species classified as tropical had a general better performance than those classified as temperate, considering short-term changes in abundance and basal area in tree communities of the Araucaria forest.

Our results in terms of species distribution along the altitudinal gradient suggest an unexpected migration trend, since 66% of species showed a downward shift of their center of gravity. As a consequence of rising temperature, plant species distributions are expected to shift toward higher elevations and this prediction has been supported by

many empirical evidences (Kelly and Goulden 2008, Lenoir et al. 2009, Feeley et al. 2011). However, most of the studies reporting upward migration also indicate that some species might migrate to lower altitudes. In a literature review, Lenoir et al. (2010) observed that, on average, 65% of the species shifted their distributions towards higher elevations, 10% did not change their distribution and 25% shifted towards lower elevations.

Patterns of downward migration have received little attention, probably because it seems to be less likely to occur as a consequence of climate change. This migration process could be generated by simple stochastic fluctuations of populations (Lenoir et al. 2010). Yet, local variation in abiotic factors such as topography, soil conditions and microclimate could create refuges for local persistence of populations even under rising temperatures (Scherrer and Körner 2011). Furthermore, land-use related to habitat modification and biotic interactions (e.g. competition, see Lenoir et al. 2010 for a review) could also be potential mechanisms for downward migration. Despite the fact that we selected areas with mature forest stands, we could still observe pioneer species occurring with high abundance as adult trees and not as saplings. These species are characterized by being light-demanding and thus dependent on gaps within mature forests to regenerate in the understory. Light-demanding species must so track to suitable sites, which might be more common on higher disturbed sites in lowlands of the Atlantic Rainforest. This seems to be the case of many pioneer species, such as *Alchornea triplinervia, Allophylus edulis, Cecropia glaziovii, Miconia cabucu, Myrsine umbellata* and *Tetrorchidium rubrivenium*.

Regarding the biotic interactions, rising temperatures are also expected to change the intensity and importance of species interactions (Hughes 2000). Ecological theory suggests that positive plant-plant interactions (e.g. facilitation) may allow species to occur at higher altitudes than it would be possible given their own ability in the absence of interactions (Roux et al. 2012). On the other hand, negative plant-plant interactions (e.g. competition) could generate displacement in species range. Species with low competitive power and with a observed distribution much below of the "total potential distribution" along the environmental gradient are especially good candidates for downward migration (Lenoir et al. 2010). Considering that increasing temperatures promotes shifts in species distribution towards higher elevations, at lower altitudes competition can be relieved. This may allow species with less competitive power to migrate downward, where they could have been excluded by better competitors (Lenoir

et al. 2010). In tropical systems where species diversity is high and competition is an important driver of species assemblage (Wright 2002), this mechanism could help to explain trends of downward migration.

Although most of the species showed a downward migration, 52 of the 103 plots demonstrated positive shifts (juvenile > adult) in the community elevation scores (CES), which indicates an upward migration. This pattern becomes more evident in plots located above the 400 meters of altitude, while below this limit the communities are showing a pattern of downward shifts. The altitudinal gradient and the associated environmental conditions produces a continuum of species turnover in the Atlantic Rainforest, where the annual minimum temperature is an important driver (Bergamin et al. 2012). The altitudinal range of 400 meters matches the limit used by IBGE (2004) for classify subtypes of the Atlantic Rainforest in the southern Brazil: sites below this altitudinal belt are classified as submontane Atlantic Rainforest (from 30 to 400 m) and above it they are classified as montane Atlantic Rainforest (from 400 to 1000 m). Thus, this altitudinal belt represents a natural boundary and communities occurring above the 400 meters of altitude, as our results indicate, seem to be more susceptible to increasing temperatures probably due to the species affinity to colder temperatures. Therefore, these communities need to migrate to higher altitudes to keep in pace with climate change. On the other hand, communities that are occurring below the altitudinal belt of 400 m may are indifferent to the increase in temperature or yet may present a downward migration trend due to the possible explanations already mentioned above (paragraphs two and three).

Regarding the short-term changes, temperate species exhibited the worse performance in almost all strata. Only in the upper stratum, the group of temperate species showed positive values for abundance and growth. Even so, its mean growth in basal area was lower then the group of tropical species. As expected, the increase in temperature seems to harm temperate species since they may perform better on colder environments. This pattern becomes more evident for the lower and the intermediate strata. Seedlings presented more mortality than recruitment and the saplings exhibited the same pattern, also demonstrating a decrease in basal area. These results indicate that species with more affinity to temperate ecosystems, as those that are indicators of the Araucaria Forest, are having difficulties to regenerate and grow especially in early life stages. This short-term dynamic may be reflecting direct effects of current climate

changes (e.g. increasing temperature) on species fitness or yet indirect effects, such as changes in competition with other groups (Davis et al. 2001).

Generalist species presented more recruitment than mortality in the lower stratum, but in the intermediate and upper strata this group exhibited an opposite pattern – the balance in abundance was negative. Generalist species are likely to exhibit broader phenotypic variability, allowing them to colonize different environments and formations (Tienderen 1997). However, some species of this group are light dependent with a shorter life cycle when compared with shade tolerant species. Therefore, mortality events of individuals from the intermediate and upper strata may be linked with successional changes in the forest. Despite this result, individuals of these species that survived over time presented positive values for growth.

As warming climate is expected to promote shifts in tree species distribution, species performance in the communities is totally linked with this process. Tropical species are migrating from the Atlantic Rainforest in the slopes and are colonizing new areas inside the Araucaria Forest. Young plants of species in the lower stratum presented a negative balance in abundance, probably due to mortality under frost events or the low temperatures during the winter. This value, however, was worst for the group of temperate species. Nevertheless, for the other two strata tropical species exhibited more recruitment than mortality and the positive growth was higher than the other groups. Thus, even the results of short-term dynamic are indicating changes probably associated to the increasing of temperature, since tropical species are establishing and growing better in the Araucaria Forest than cold-adapted species (temperate group).

Conclusion

In this paper we showed how climate change is affecting the distribution and performance of tree species in southern Atlantic Forest. Overall, species are responding idiosyncratically to the ongoing temperature increase. Species adapted to higher altitudes are being more affected and, as a consequence, they have to shift their distribution towards colder areas to remain within their thermal niches. The migration depends on successful dispersal and establishment of species to new areas. The failure represents range contractions, and consequently, raises their extinction risk. Beyond the failure, time lag responses in plant dispersal due to climate change also increase the extinction risk. In this context, downward migration patterns could be a consequence of failure or time lag to migrate and establish, probably due to frost frequency or extreme

events as snow falls, as observed in Santa Catarina in the winter of 2013. These events increase the probability of mortality mainly for lowland species (typical tropical species) in areas of transitional climate conditions. Furthermore, species depend on the availability of new areas to colonize. For species occurring at the end of the altitudinal gradient and adapted to cold climates, this may mean nowhere to migrate. On the other hand, there are species that are benefiting with rising temperatures, such as those of the tropical group. These species are showing a better performance in short-term dynamics than temperate species in areas of high altitude (around 900 m) in the Araucaria Forest.

Finally, the monitoring of permanent plots in such ecotonal areas of the Atlantic Forest are essential to understand the consequences of climate change and to mitigate its effect on this biodiversity hotspot. Species will respond in different ways and thus, identify which species will be more threatened is indispensable to conservation actions. Climate change impacts are far from being in one direction only and early expectations that climate warming will result in upward shifts doe not always match. The mechanisms behind downward migrations are unclear and further studies are necessary to disentangle this complex movement. Yet, future studies based on the description of time series coupled with modeling techniques will increase accuracy of such changes to the future predictions.

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CONSIDERAÇÕES FINAIS

Com os resultados desta tese, mostramos a importância de considerar os padrões espaço-temporais de distribuição de espécies sob uma perspectiva de planejamento de conservação e mudanças climáticas. Com relação ao planejamento de conservação, considerar a beta diversidade, principalmente quando o *turnover* de espécies é predominante, para a expansão de áreas protegidas em uma região é crucial para maximizar conservação da diversidade gama. Regiões com elevado *turnover* necessitam que as áreas protegidas estejam próximas uma das outras. Este é o caso da Mata Atlântica no sul do Brasil, pois as formações florestais presentes neste bioma apresentaram altas taxa de beta diversidade e um decaimento na similaridade de espécies arbóreas mesmo em pequenas distâncias. Além disso, as formações florestais estudadas exibiram altas taxas de desmatamento, principalmente a Floresta com Araucária e a Floresta Estacional. Ainda, ambas as florestas apresentaram resultados preocupantes quanto à porcentagem de remanescentes protegidos, o que lhes confere um alto valor de risco de conservação. A grande maioria das áreas protegidas está concentrada na Floresta Atlântica *stricto sensu*, provavelmente devido a maior riqueza de espécies de árvores descrita para esta formação. Porém, altos valores de beta diversidade foram encontrados para as três formações florestais, e levando em conta a perda de hábitat e a porcentagem de remanescentes protegidos, recomendamos fortemente que a rede de áreas protegidas seja expandida na Floresta com Araucária e Floresta Estacional.

A proximidade de áreas protegidas, além de ser importante para maximizar a conservação da diversidade gama, é crucial para garantir a migração das espécies. As mudanças climáticas tem causado mudanças na distribuição das espécies, forçando estas a migrarem para se manterem dentro de seus limites ecológicos. Como podemos observar no capítulo três, as flutuações climáticas que ocorreram no passado tiveram um importante papel na retração da Floresta com Araucária, e consequentemente uma expansão de outras formações florestais dado o aumento da temperatura. Assim, as espécies que compõem a Floresta com Araucária tiveram que migrar para estarem dentro dos seus limites ecológicos, causando mudanças na composição de espécies através do tempo. Também podemos observar que futuramente, se a temperatura continuar aumentando como é esperado, a Floresta com Araucária sofrerá uma drástica redução na sua distribuição. Este fato pode ser corroborado pelos resultados encontrados no capítulo quatro, já que grupos de espécies na Floresta Atlântica estão migrando em

direção a áreas de maior altitude, ou seja mais frias, onde está a Floresta com Araucária. Além disso, observamos que espécies da Floresta Atlântica que já alcançaram áreas de Floresta com Araucária, além de estarem se estabelecendo, estão conseguindo obter maiores taxas de recrutamento e crescimento e menor mortalidade que espécies características da Floresta com Araucária. Este processo com certeza desencadeará uma migração destas espécies para novos hábitats. Porém, e se estas espécies não tiverem mais para onde ir?

Para finalizar, saliento a importância de futuros estudos nesta linha de mudanças espaço-temporais na composição de espécies como subsídio para planejamento de conservação, juntamente com os efeitos que as mudanças climáticas terão sobre as mudanças na distribuição geográficas das espécies. A compreensão destes efeitos é considerada dentre os desafios mais urgentes enfrentados pela comunidade científica a fim de criar estratégias eficientes para minimizar e mitigar os efeitos de mudanças climáticas. Expandir rede de áreas protegidas é crucial para possibilitar a migração das espécies, bem como, proteger ou restaurar novas áreas para onde as espécies migrarão futuramente. Ainda, contínuos monitoramentos para investigar mudanças na demografia das espécies de plantas no tempo em parcelas permanentes, juntamente com os modelos de nicho ecológico, podem elucidar os padrões de respostas destas espécies frente às previsões de aumento da temperatura. Por fim, uma vez que as espécies de plantas responderão de diferentes maneiras frente as mudanças climáticas, identificar quais espécies estarão mais ameaçadas é indispensável para ações de conservação.

MATERIAL SUPLEMENTAR

CAPÍTULO 1

Compilation of Woody Species Occurring in Brazilian Atlantic Forest Complex

Appendix 1: List of publications from which data were obtained (Para acessar a lista de referências bibliográficas, acessar o link do artigo http://escholarship.org/uc/item/2xf850wt).

Appendix 2: Photos showing the different aspects of the vegetation types in the Atlantic Forest biome

a)

b)

c)

d)

e)

f)

Photos showing the different aspects of the vegetation types in the Atlantic Forest biome: **a-b** Dense Forest; **c-d** Mixed Forest; **e-f** Seasonal Forest. The photos **e** and **f** were kindly provided by João André Jarenkow and Sandra Müller.

Appendix 3: Matrix containig the occurrence of 1,917 species per 206 sites (Para acessar a matriz de espécies por sítios, acessar o link do artigo http://escholarship.org/uc/item/2xf850wt).

Appendix 4: Information about the 206 floristic checklists (Para acessar a informação de cada sítio, acessar o link do artigo http://escholarship.org/uc/item/2xf850wt).

CAPÍTULO 2

Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Forest

Table S1 – Characteristics of the Southern Brazilian Atlantic forests sites that were used in the analysis.

Vegetation type	Site	State	Coordinates		Inclusion criteria	Method	Effort	Source
			Latitude	Longitude				
Araucaria Forest	São Francisco de Paula	RS	29º 29' S	50º 12' W	*DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	São Francisco de Paula	RS	29º 29' S	50º 11' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	São Francisco de Paula	RS	29º 29' S	50º 13' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	São Francisco de Paula	RS	29º 24' S	50º 23' W	Tree spp with ≥ 2 m tall	Plot	972 m²	Rosário (2001)
	São Francisco de Paula	RS	29º 02' S	50º 23' W	**GBH ≥ 30 cm	Plot	9990 m²	Longui *et al.* (2006)
	São Francisco de Paula	RS	29º 25' S	50º 23' W	DBH ≥ 5 cm	Plot	2900 m²	Sonego et al. (2007)
	São Francisco de Paula	RS	29º 23' S	50º 14' W	DBH ≥ 10 cm	Plot	12000 m²	Bergamin et al. (2010)
	São Francisco de Paula	RS	29º 22' S	50º 14' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin et al. (2010)
	São Francisco de Paula	RS	29º 22' S	50º 15' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin et al. (2010)
	Nova Petrópolis	RS	29° 22' S	51° 05' W	Tree spp. with DBH ≥ 5 cm and > 4 m tall	Floristic inventory	***Na	Grings & Brack (2009)
	Cambará do Sul	RS	29º 10' S	50º 07' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	Cambará do Sul	RS	29º 10' S	50º 05' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	Cambará do Sul	RS	29º 09' S	50º 05' W	DBH ≥ 10 cm	Plot	1200 m²	Bergamin (2010)
	Caxias do Sul	RS	29º 00' S	50º 55' W	DBH† ≥ 5 cm	Plot	8000 m²	Rondon Neto *et al.* (2002)
	Nova Prata	RS	28º 56' S	51º 53' W	GBH ≥ 30 cm	Plot	10000 m²	Nascimento *et al.* (2001)
	Vacaria	RS	28º 40' S	50º 56' W	>2 m tall	Plot	2500 m²	Mauhs & Backes (2002)
	Bom Jardim da Serra	SC	28º 19' S	49º 33' W	All tree spp.	Floristic inventory	Na	Eskuche (2007)
	Muitos Capões	RS	28º 13' S	51º 10' W	DBH ≥ 5 cm	Plot	4800 m²	Jarenkow & Baptista (1987)
	Campo Belo do Sul	SC	28º 00' S	50º 49' W	DBH ≥ 10 cm	Plot	9600 m²	Formento *et al.* (2004)
	Faxinalzinho	SC	27º 20' S	52º 40' W	GBH ≥ 15 cm	Plot	10000 m²	Leyser et al. (2009)
	Caçador	SC	26º 50' S	50º 55' W	Tree spp. with > 60 cm tall	Plot	10000 m²	Silva *et al.* (1997)
	Caçador	SC	26º 47' S	51º 01' W	DBH ≥ 5 cm	Point centered quarter method	600 points	Negrelle & Silva (1992)
	Lages	SC	27° 47' S	50° 21' W	DBH ≥ 5cm	Plot	1600m²	Klauberg et al. (2010)
	Urupema	SC	27° 52' S	49° 55' W	All tree spp.	Floristic inventory	Na	Martins-ramos et al. (2010)
Atlantic Forest *s.s.*	Blumenau	SC	27º 03' S	49º 04' W	DBH ≥ 4.8 cm	Plot	4000 m²	Schorn (2005)
	Governador Celso Ramos	SC	27º 18' S	48º 33' W	Tree spp. with ≥ 1 m tall	Plot	2500 m²	Citadini-Zanette et al. (2001
	São Pedro de Alcântara	SC	27º 34' S	48º 48' W	Tree spp. with ≥ 1 m tall	Plot	6000 m²	Siminiski et al. (2004)
	Siderópolis	SC	28º 34' S	49º 24' W	DBH ≥ 5 cm	Plot	10000 m²	Martins (2005)
	Criciúma	SC	28º 48' S	49º 25' W	DBH ≥ 5 cm	Plot	10000 m²	Silva (2006)
	Palmares	RS	30º 21' S	50º 20' W	DBH ≥ 5 cm	Point centered quarter method	30 points	Moraes & Mondin (2001)
	Lagoa peixe	RS	31º 10' S	50º 47' W	DBH ≥ 5 cm	Point centered quarter method	60 points	Dorneles & Waechter (2004

	Dom Pedro de alcântara	RS	29º 23' S	49º 05' W	GBH ≥ 15 cm	Point centered quarter method	125 points	Nunes (2001)
	Morrinhos do Sul	RS	29º 21' S	49º 58' W	DBH ≥ 5 cm	Plot	10000 m²	Jarenkow (1994)
	Parque Estadual de Itapeva	RS	29º 21' S	49º 45' W	DBH ≥ 2.5 cm	Plot	1000 m²	Kindel (2002)
	Riozinho	RS	29º 36' S	50º 22' W	DBH ≥ 5 cm	Plot	10000 m²	Brack (2002)
	Maquiné	RS	29º 42' S	50º 09' W	DBH ≥ 5 cm	Plot	10000 m²	Brack (2002)
	São Francisco de Paula	RS	29º 28' S	50º 09' W	DBH ≥ 10 cm	Plot	4200 m²	Mello (2006)
	São Francisco de Paula	RS	29º 29' S	50º 11' W	DBH ≥ 10 cm	Plot	4200 m²	Mello (2006)
	Terra de Areia	RS	29° 38' S	50° 08' W	DBH ≥ 5cm	Plot	2400m²	Molz (2011)
	Terra de Areia	RS	29° 38' S	50° 08' W	DBH ≥ 5cm	Plot	2400m²	Molz (2011)
	Terra de Areia	RS	29° 38' S	50° 08' W	DBH ≥ 5cm	Plot	2400m²	Molz (2011)
	Terra de Areia	RS	29° 37' S	50° 19' W	DBH ≥ 5cm	Plot	5000m²	Junior (2011)
	Maquiné	RS	29° 39' S	50° 13' W	DBH ≥ 10 cm	Plot	1200m²	Zanini (2011)
	Maquiné	RS	29° 55' S	50° 18' W	DBH ≥ 10 cm	Plot	1200m²	Zanini (2011)
	Maquiné	RS	29° 54' S	50° 04' W	DBH ≥ 10 cm	Plot	1200m²	Zanini (2011)
Seasonal Forest								
	São Martinho da Serra	RS	29° 32' S	53° 48' W	GBH ≥ 30 cm	Plot	2800m²	Scipioni et al. (2009)
	Cachoeira do Sul	RS	30° 04' S	52° 53' W	DBH ≥ 5 cm	Plot	5800m²	Araujo et al. (2004)
	Santa Teresa	RS	29° 11' S	51° 43' W	DBH ≥ 9.5 cm	Plot	4000m²	Vaccaro (1991)
	Parobé	RS	29° 41' S	50° 51' W	DBH≥ 10 cm	Point centered quarter method	30 points	Daniel (1991)
	Turvo	RS	27° 11' S	53° 51' W	DBH ≥ 5 cm	Point centered quarter method	140 points	Ruschel et al. (2007)
	Cristal	RS	31° 01' S	51° 56' W	DBH ≥ 5 cm	Plot	10000m²	Marchi & Jarenkow (2008)
	Jaguari	RS	29° 30' S	54° 40' W	DBH≥ 10 cm	Plot	14000m²	Longhi et al. (2005)
	Parobé	RS	29° 42' S	50° 51' W	DBH ≥ 5 cm	Plot	2600m²	Porto et al. (2008)
	Santa Maria	RS	29° 43' S	53° 43' W	DBH ≥ 9.5 cm	Plot	10500m²	Farias et al. (1994)
	Turvo	RS	27° 09' S	53° 53' W	DBH ≥ 5 cm	Plot	10000m²	Giehl & Jarenkow (2008)
	Santa Maria	RS	29° 41' S	53° 47' W	DBH ≥ 5 cm	Plot	3600m²	Longhi et al. (1999)
	Santa Maria	RS	29° 43' S	53° 47' W	DBH ≥ 9.5 cm	Plot	3200m²	Longhi et al. (2000)
	Santa Maria	RS	29° 45' S	53° 45' W	DBH ≥ 5 cm	Plot	10000m²	Budke et al. (2004)
	Arroio do Padre	RS	31° 27' S	52° 28' W	DBH≥ 10 cm	Plot	10000m²	Souza (2001)
	Bossoroca	RS	28° 42' S	54° 53' W	DBH≥ 10 cm	Plot	7000m²	Boligon et al. (2005)
	Camaqua	RS	30° 41' S	51° 53' W	DBH ≥ 5 cm	Plot	10000m²	Jurinitz & Jarenkow (2003)
	Canela	RS	29° 23' S	50° 41' W	DBH≥ 10 cm	Point centered quarter method	30 points	Daniel (1991)
	Tupanciretã	RS	29° 04' S	53° 50' W	DBH ≥ 5 cm	Plot	2000m²	Rosa et al. (2008)
	Encruzilhada do Sul	RS	30° 30' S	52° 42' W	DBH ≥ 5 cm	Plot	3000m²	Giongo & Waechter (2007)
	Jaguari	RS	29° 30' S	54° 40' W	DBH≥ 10 cm	Plot	14000m²	Hack et al. (2005)
	Cachoeira do Sul	RS	30° 00' S	52° 48' W	DBH ≥ 5 cm	Plot	10000m²	Lindenmaier & Budke (2006
	Monte Negro	RS	29° 49' S	51° 25' W	DBH ≥ 5 cm	Plot	18000m²	Longhi et al. (2008)
	Rolante	RS	29° 35' S	50° 26' W	DBH≥ 10 cm	Point centered quarter method	30 points	Daniel (1991)
	Santiago	RS	29° 10' S	54° 51' W	DBH ≥ 9.5 cm	Plot	Na	Longhi (1991)
	São Jerônimo	RS	30° 03' S	51° 43' W	DBH≥ 10 cm	Plot	2400m²	Balbueno & Oliveira (2000)
	Arroio dos Ratos	RS	30° 11' S	51° 45' W	DBH≥ 10 cm	Plot	2400m²	Balbueno & Oliveira (2000)
	São Sepé	RS	30° 10' S	53° 34' W	DBH≥ 10 cm	Plot	2500m²	Longhi et al. (1992)
	Vale do Sol	RS	29° 34' S	52° 40' W	DBH ≥ 5cm and high ≥ 5m	Plot	10000m²	Jarenkow & Waechter (2001
	Itapiranga	SC	27° 11' S	53° 38' W	DBH ≥ 5 cm	Plot	11200m²	Ruschel et al. (2009)
	São Valentim	SC	26° 56' S	53° 31' W	DBH ≥ 5 cm	Plot	11200m²	Ruschel et al. (2009)
	Sinimbú	RS	29° 23' S	52° 32' W	DBH≥ 4.8 cm	Plot	10000m²	Sühs and Budke (2011)

Santo Ângelo	RS	28° 19' S	54° 15' W	DBH≥ 10 cm	Plot	2400m²	Hüller et al. (2011)

* DBH: Diameter at breast height

** GBH: Girth at breast height

*** Na: Not available

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CAPÍTULO 3

New insights about the dynamics of Araucaria forest through time

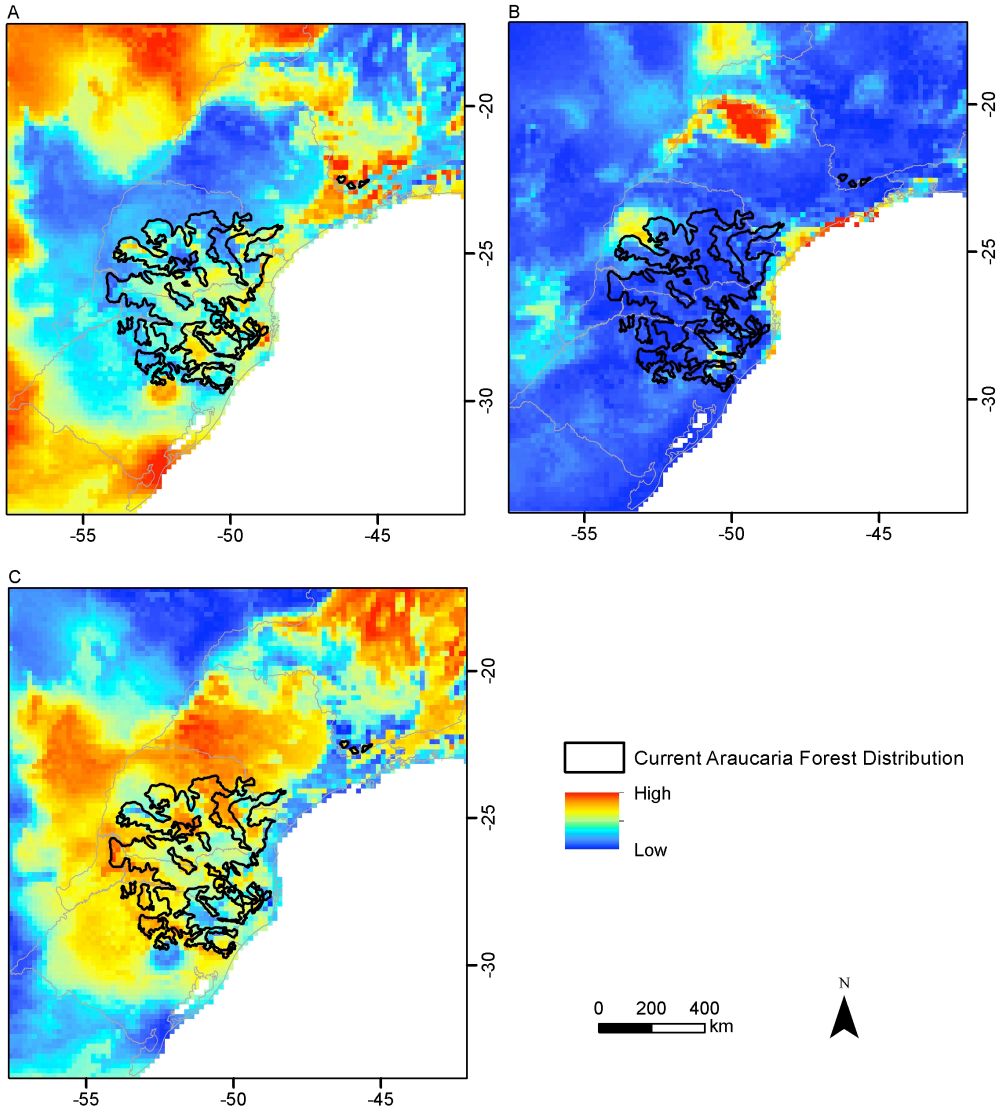

Figure S1: Maps of variance component for the vegetation map approach: A- Ecological Niche Models; B- Atmosphere-Ocean Global Circulation Models (AOGCMs); C- Time.

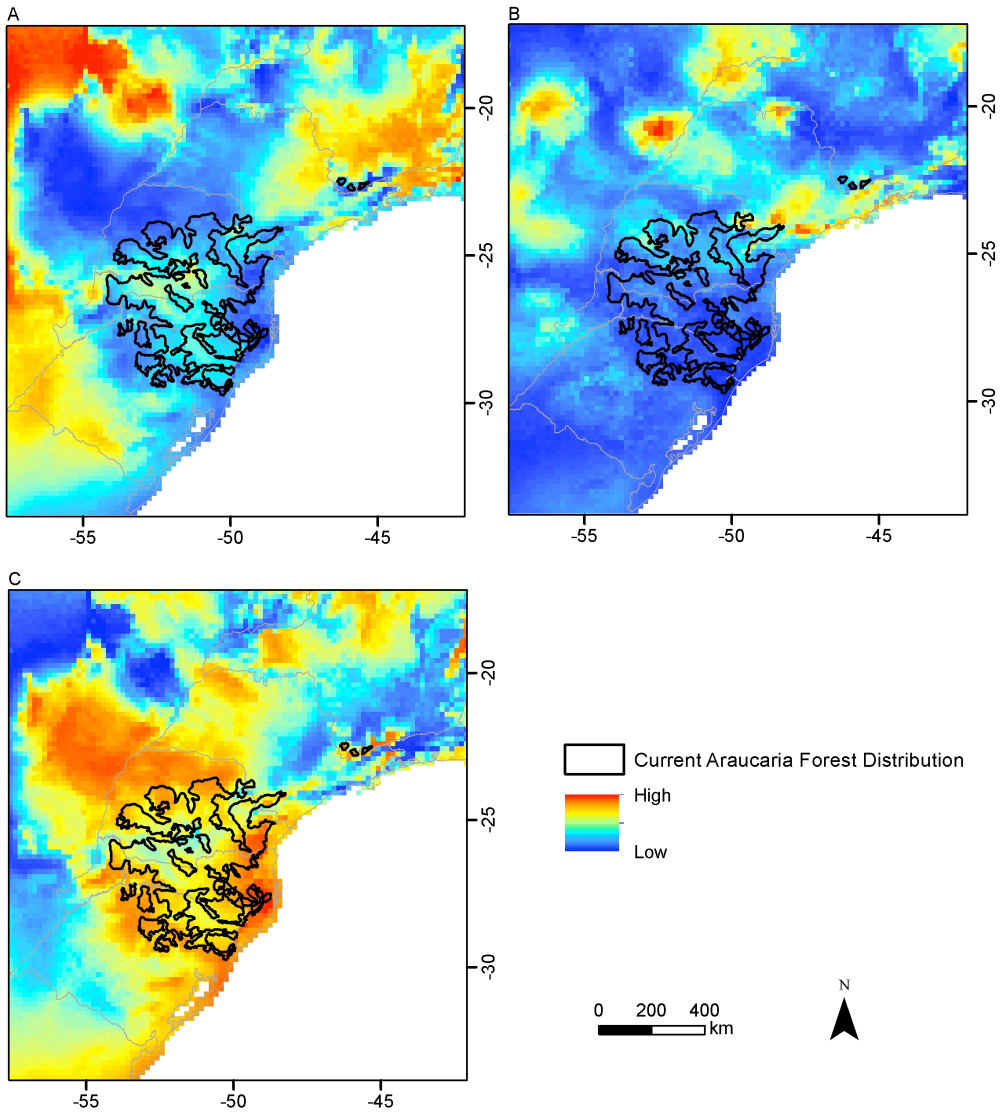

Figure S2: Maps of variance component for the species approach: A- Ecological Niche Models; B- Atmosphere-Ocean Global Circulation Models (AOGCMs); C- Time.

Table S1: Comparison between model predictions and pollen studies for the LGM (21.000 years before present). Code refer to localities indicated in Fig. 4A and 4B.

Site	Coordinates	Altitude	Code	Presence of pollen from Araucaria	Match with the model?	Reference
Cambará do Sul, State of Rio Grande do Sul	29°03'09" S, 50°06'04" W	1040 m	1	Yes	Yes	Behling et al. 2004
São Francisco de Assis, State of Rio Grande do Sul	29°35'12" S, 55°13'02" W	100 m	2	No	Yes	Behling et al. 2005
Morro Itapeva, State of São Paulo	22°47' S, 45°32' W	1850 m	3	Yes	Yes	Behling 1997
Serra da Bocaina, State of São Paulo and Rio de	22°44'30" S, 44°33'24" W	1500 m	4	Yes	Yes	Behling et al. 2007
Volta Velha, State of Santa Catarina	26°04' S, 48°38 W	5 m	6	No	Yes	Behling & Negrelle 2001
Serra do Tabuleiro, State of Santa Catarina	27°53'48.46" S, 48°52'5.33" W	860 m	8	Yes	Yes	Jeske-Pieruschka et al. 2012
Serra do Mar, State of São Paulo	23°56' S, 46°39' W	800 m	11	Yes	Yes	Pessenda et al. 2009
São Francisco de Paula, State of Rio Grande do Sul	29°29'35" S, 50°37'18" W	880 m	12	Yes	Yes	Leonhardt & Lorscheitter 2010
Ilha do Cardoso, State of São Paulo	25°05' S, 47°56' W	sea level	13	Yes	No	Pessenda et al. 2012
Salitre, State of Minas Gerais	19° S, 46°46' W	1050 m	14	Yes	Yes	Ledru 1993
Catas Altas, State of Minas Gerais	20°05' S, 43°22' W	755 m	15	Yes	Yes	Behling & Litche 1997

Table S1: Comparison between model predictions and pollen studies for the mid-Holocene (6.000 years before present). Code refer to localities indicated in Fig. 4C and 4D.

Site	Coordinates	Altitude	Code	Presence of pollen from Araucaria Forest	Match with the model?	Reference
Cambará do Sul, State of Rio Grande do Sul	29°03'09" S, 50°06'04" W	1040 m	1	Yes	Yes	Behling et al. 2004
São Francisco de Assis, State of Rio Grande do Sul	29°35'12" S, 55°13'02" W	100 m	2	No	Yes	Behling et al. 2005
Morro Itapeva, State of São Paulo	22°47' S, 45°32' W	1850 m	3	Yes	Yes	Behling 1997
Serra da Bocaina, State of São Paulo and Rio de Janeiro	22°42'50" S, 44°34 W	1500 m	4	Yes	Yes	Behling et al. 2007
Lago dos Pires, State of Minas Gerais	17°57'S, 42°13'W	390 m	5	No	Yes	Behling 1995
Volta Velha, State of Santa Catarina	26°04' S, 48°38 W	5 m	6	Yes	No	Behling & Negrelle 2001
Jacareí, State of São Paulo	23°17'S, 45°58'W	550 m	7	Yes	Yes	Garcia et al. 2004
Serra do Tabuleiro, State of Santa Catarina	27°53'48.46" S, 48°52'5.33" W	860 m	8	Yes	Yes	Jeske-Pieruschka et al. 2012
Santo Antônio da Patrulha, State of Rio Grande do Sul	29°44'45" S, 50°32'56" W	37 m	9	Yes	Yes	Macedo et al. 2010
São Francisco de Paula, State of Rio Grande do Sul	29°28′35″S, 50°34′22″W	895 m	10	Yes	Yes	Jeske-Pieruschka et al. 2011
São Francisco de Paula, State of Rio Grande do Sul	29°29'35" S, 50°37'18" W	880 m	12	Yes	Yes	Leonhardt & Lorscheitter 2010
Salitre, State of Minas Gerais	19° S, 46°46' W	1050 m	14	No	Yes	Ledru 1993
Lagoa Nova, State of Minas Gerais	17°58' S, 42°12' W	390 m	16	No	Yes	Behling 2003
Serra dos Campos Gerais, State of Paraná	24°40' S, 50°13'W	1200 m	17	Yes	Yes	Behling 1997

CAPÍTULO 4

Contrasting responses of tree species in face of climate change in Atlantic Forest ecotones: migrations trends and short-term dynamics

This classification method proposed by Chazdon et al (2011) employs multinomial models based on estimated relative abundance of species in two habitats and then classify the species into four groups: in our case (1) specialists of Atlantic Rainforest, (2) specialists of Araucaria Forest, (3) generalists and (4) species to rare to classify. We use the same matrix of species per forest type that Bergamin et al. (2012) used. However, this classification method has advantages in relation to indicator species analysis (Dufrene and Legendre 1997) used by Bergamin et al. (2012) due to considerer the classification of habitat specialists and the capacity to distinguish habitat generalists from species that are too rare to classify (Chazdon et al. 2011). The classification of species into groups was performed in R, with package vegan (Oksanen etal. 2007).

Table S1: Species classification into generalist, temperate and tropical group and the performance of each species for the different strata.

Lower strata

Species	Habitat type	Δ Species abundance
Annona rugulosa	Generalist	0.00
Blepharocalix salicifolius	Generalist	0.00
Casearia decandra	Generalist	0.04
Cryptocaria aschersoniana	Generalist	0.09
Dasyphyllum spinesc ns	Generalist	0.00
Eugenia handroi	Generalist	-0.07
Eugenia subterminalis	Generalist	0.12
Ilex paraguariensis	Generalist	-0.08
Laplacea acutifolia	Generalist	0.20
Myrceugenia miersiana	Generalist	0.07
Myrceugenia myrcioides	Generalist	0.01
Myrcia oligantha	Generalist	-0.02
Myrciaria floribunda	Generalist	0.12
Myrsine lorentziana	Generalist	-0.03
Nectandra grandiflora	Generalist	-0.01
Ocotea porosa	Generalist	0.00
Prunus myrtifolia	Generalist	0.00
Vernonanthura discolor	Generalist	0.00
Weinmannia paulliniifolia	Generalist	0.12
Xylosma pseudosalzmanii	Generalist	0.04
Zanthoxylum rhoifolium	Generalist	0.00
Araucaria angustifolia	Temperate	-0.23

Drimys angustifolia	Temperate	-0.12
Ilex microdonta	Temperate	0.02
Myrceugenia euosma	Temperate	-0.10
Myrceugenia mesomischa	Temperate	-0.12
Myrcia guianensis	Temperate	-0.15
Myrcia lajeana	Temperate	0.00
Myrcia retorta	Temperate	-0.07
Ocotea elegans	Temperate	-0.47
Podocarpus lambertii	Temperate	0.27
Cabralea canjerana	Tropical	0.12
Calyptranthes grandifolia	Tropical	0.00
Casearia obliqua	Tropical	0.00
Cupania vernalis	Tropical	-0.12
Daphnopsis fasciculata	Tropical	-0.09
Lamanonia ternata	Tropical	0.00
Matayba elaeagnoides	Tropical	-0.05
Piptocarpha axillaris	Tropical	-0.21
Psychotria suterella	Tropical	0.07

Intermediate stratum

Species	Habitat type	Δ Species abundace	Δ Species basal area
Annona rugulosa	Generalist	-0.05	-0.16
Blepharocalyx salicifolius	Generalist	0.00	0.14
Calyptranthes concinna	Generalist	-0.05	-0.23
Casearia decandra	Generalist	0.00	0.08
Cryptocarya aschersoniana	Generalist	0.00	0.05
Eugenia handroi	Generalist	0.05	0.14
Eugenia subterminalis	Generalist	0.00	-0.03
Ilex paraguariensis	Generalist	0.07	0.17
Laplacea acutifolia	Generalist	-0.12	0.08
Myrceugenia miersiana	Generalist	0.05	0.02
Myrceugenia myrcioides	Generalist	-0.03	-0.03
Myrcia oligantha	Generalist	0.03	-0.02
Myrciaria floribunda	Generalist	0.00	0.04
Myrsine lorentziana	Generalist	-0.03	0.00
Nectandra grandiflora	Generalist	0.01	-0.02
Ocotea porosa	Generalist	0.00	0.01
Prunus myrtifolia	Generalist	-0.07	0.04
Sapium glandulosum	Generalist	0.05	0.16
Tibouchina sellowiana	Generalist	-0.12	0.40
Vernonanthura discolor	Generalist	0.00	0.07
Weinmannia paulliniifolia	Generalist	0.04	0.08
Xylosma pseudosalzmanii	Generalist	0.00	0.02
Zanthoxylum rhoifolium	Generalist	-0.18	0.01
Araucaria angustifolia	Temperate	-0.12	-0.13

Drimys angustifolia	Temperate	-0.10	-0.06
Ilex microdonta	Temperate	-0.14	-0.14
Myrceugenia euosma	Temperate	-0.03	0.03
Myrceugenia mesomischa	Temperate	0.01	-0.04
Myrcia guianensis	Temperate	0.00	-0.05
Myrcia lajeana	Temperate	0.00	0.02
Myrcia retorta	Temperate	-0.04	0.01
Ocotea elegans	Temperate	0.02	-0.02
Podocarpus lambertii	Temperate	-0.04	-0.06
Siphoneugena reitzii	Temperate	-0.04	-0.01
Cabralea canjerana	Tropical	0.12	0.29
Calyptranthes grandifolia	Tropical	0.03	0.09
Cedrela fissilis	Tropical	0.00	0.05
Cinnamomum glaziovii	Tropical	0.04	0.26
Cupania vernalis	Tropical	0.00	0.07
Daphnopsis fasciculata	Tropical	-0.02	0.01
Lamanonia ternata	Tropical	0.00	0.13
Matayba elaeagnoides	Tropical	-0.12	-0.06
Myrceugenia ovata	Tropical	0.00	0.14
Piptocarpha axillaris	Tropical	-0.02	0.02
Psychotria suterella	Tropical	0.00	0.21
Roupala brasiliensis	Tropical	0.00	0.00

Upper stratum

Species	Habitat type	Δ Species abundance	Δ Species basal area
Allophylus edulis	Generalist	0.12	0.09
Blepharocalix salicifolius	Generalist	-0.12	-0.27
Calyptranthes concinna	Generalist	-0.04	-0.01
Casearia decandra	Generalist	0.00	0.00
Cryptocaria aschersoniana	Generalist	-0.05	-0.08
Eugenia handroi	Generalist	-0.01	-0.03
Eugenia subterminalis	Generalist	0.02	-0.02
Ilex paraguariensis	Generalist	-0.03	-0.05
Laplacea acutifolia	Generalist	0.01	0.06
Myrceugenia miersiana	Generalist	0.06	-0.08
Myrceugenia myrcioides	Generalist	-0.02	0.03
Myrcia oligantha	Generalist	-0.14	-0.10
Myrciaria floribunda	Generalist	-0.02	0.00
Myrsine lorentziana	Generalist	0.00	-0.04
Nectandra grandiflora	Generalist	0.02	0.04
Ocotea porosa	Generalist	-0.02	0.02
Prunus myrtifolia	Generalist	-0.18	-0.10
Sapium glandulosum	Generalist	0.04	0.10
Tibouchina sellowiana	Generalist	-0.18	1.07
Vernonanthura discolor	Generalist	-0.12	-0.02

Weinmannia paulliniifolia	Generalist	0.08	0.01
Xylosma pseudosalzmanii	Generalist	-0.07	0.00
Zanthoxylum rhoifolium	Generalist	0.00	-0.07
Araucaria angustifolia	Temperate	0.01	0.05
Cinnamomum amoenum	Temperate	0.00	0.03
Drimys angustifolia	Temperate	-0.06	0.07
Ilex microdonta	Temperate	0.01	0.01
Myrceugenia euosma	Temperate	0.00	-0.01
Myrceugenia mesomischa	Temperate	0.03	0.15
Myrcia guianensis	Temperate	-0.05	0.01
Myrcia lajeana	Temperate	0.12	0.05
Myrcia retorta	Temperate	-0.01	-0.02
Ocotea elegans	Temperate	-0.08	-0.05
Ocotea pulchella	Temperate	0.07	-0.04
Podocarpus lambertii	Temperate	0.12	0.21
Siphoneugena reitzii	Temperate	0.00	-0.01
Cedrela fissilis	Tropical	0.00	0.01
Cinnamomum glaziovii	Tropical	0.00	0.74
Daphnopsis fasciculata	Tropical	-0.12	-0.19
Lamanonia ternata	Tropical	0.12	0.15
Piptocarpha axillaris	Tropical	0.09	0.02
Roupala brasiliensis	Tropical	0.00	0.01

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